Hydrodynamics and zooplankton ecology in the Tamar Estuary, northern Tasmania, with special emphasis on larval fishes

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Declarations

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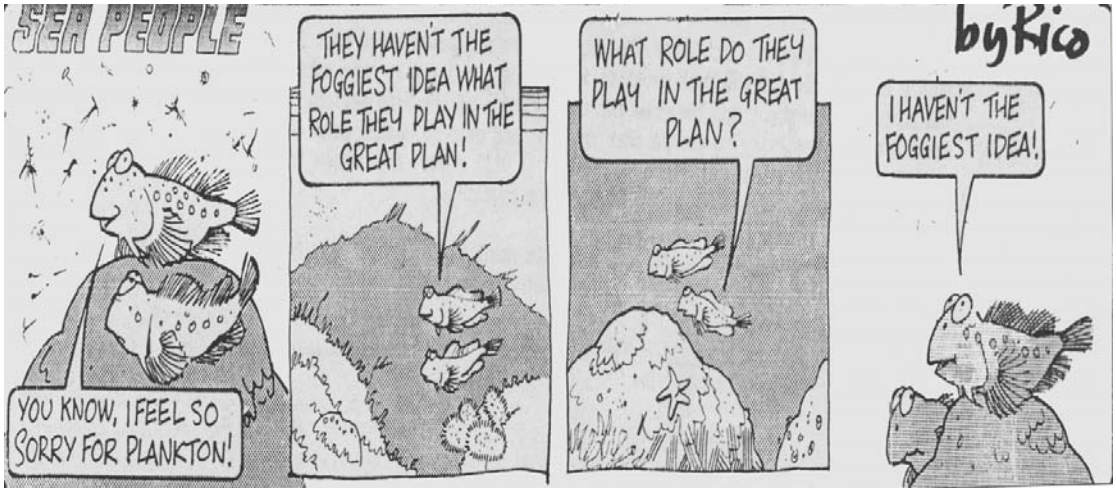
SEA PEOPLE
YOU KNOW, I FEEL SO SORRY FOR PLANKTON!
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WHAT ROLE DO THEY PLAY IN THE GREAT PLAN?
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General abstract

This thesis describes results of a comprehensive study of the Tamar Estuary, a highly-flushed system in northern Tasmania, conducted to investigate the link between hydrodynamic processes and zooplankton biomass with particular emphasis on larval fish dynamics. It comprised extensive plankton sampling together with measurements of physical parameters, between October 2001 and November 2002, including three 24-hour sampling sessions in the lower estuary to ascertain the effect of tidal currents in the transport of fishes. The Tamar was classified as a partially mixed estuary (Type 2a), based on salinity distribution, current velocities and freshwater flow. The weak vertical temperature and salinity stratification, together with strong mean current velocities (2 m/s), indicated a lack of two-layered circulation, and hence absence of a net upstream flow along the bottom. The study yielded 80,837 larval fishes representing 44 families, with catches dominated by gobiids, blenniids, clinids and engraulids. Temperature was found to be the most important variable driving temporal changes in zooplankton biomass and larval concentrations. Peaks in zooplankton biomass and larval concentrations occurred simultaneously in November, both in 2001 and 2002, at temperatures ~15^{o}C, and lasted ~2 months. Results suggest that the commencement and intensity of spawning in the Tamar may be triggered by changes in abiotic factors, such as increasing temperature and moderate freshwater flow, whereas spawning duration may be linked to biotic factors such as the presence of potential predators and food availability. No evident pattern in the spatial distribution, both of zooplankton biomass and larval fishes was observed during the peak abundance period. The spatial structuring of the larval assemblage was driven by salinity, with one assemblage representing mostly estuarine-spawned larvae (mouth to

35 km upstream), and the other representing larvae of freshwater taxa (>35 km). The geographical extent of each assemblage could be associated with the strong diffusive forces of tidal currents, which also affected zooplankton biomass. An estuarine transport model used to investigate fish movements along the lower estuary was able to accurately predict concentrations of virtual larvae early in the season, as they behaved similar to passive particles. However, it was unable to accurately predict concentrations later in the season, likely because most larvae were displaying a behaviour different to passive particles due to increased swimming ability. Strategies likely helping retention and survival of larvae in the Tamar Estuary include a short (~2 months), defined occurrence period that is well-timed with zooplankton production, and location where these larvae are spawned within the estuary.

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The first three years of this study were undertaken at the Australian Maritime College, after which I transferred to the University of Tasmania to finalize the study. I would like to thank the Australian Maritime College for their support during the first three years of this work.

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Contents

Chapter 1

General introduction

1.1 The role of estuaries in larval fish dynamics

Estuaries are complex, dynamic and biotically rich systems with a mosaic of spatially and temporally variable habitats, which are recognized amongst the most productive aquatic ecosystems in the world, having exceptionally high levels of primary and secondary production (Lauff, 1967; McLusky, 1981; Lewis and Platt, 1982; Ketchum, 1983; Day *et al.*, 1989; Potter *et al.*, 1990; Whitfield, 1999; Peterson *et al.*, 2004). This high productivity is due to the interaction of high nutrient inputs from anthropogenic activities and natural processes, effective tidal mixing and retention of nutrients, physical discontinuities forced by freshwater-saltwater interfaces, complex bathymetries and salinity gradients (Largier, 1993; Roman *et al.*, 2001; Jung and Houde, 2003). It is this high productivity the reason why many fish species worldwide utilize these systems as nursery and spawning grounds (Roper, 1986; Potter *et al.*, 1990; Whitfield, 1999).

The use of estuaries by fishes is greatly limited by strong salinity, temperature, dissolved oxygen and turbidity gradients which are typical of these unstable systems, and it is often euryhaline species, that are able to take advantage of the high food supply and shelter that estuaries provide (Dando, 1984; Day *et al.*, 1989; Potter *et al.*, 1990; Whitfield, 1999; Peterson *et al.*, 2004). Consequently, estuarine systems are generally characterized by a low ichthyofaunal diversity but high abundances of a few individual taxa (Potter *et al.*, 1990; Neira *et al.*, 1992; Neira and Potter, 1994; Whitfield, 1999).

The role played by estuaries in the life cycle of fish species can be of such importance that many species are regarded as estuarine-dependent (Potter *et al.*, 1990; Whitfield, 1999). In general, two main early life history strategies are evident among estuarine-dependent species, namely: a) those that enter estuaries from adjacent marine environments as larvae and/or juveniles; and b) those which are spawned within the estuary and either complete their life cycle within it or leave at a later stage (Beckley, 1985; Lenanton and Potter, 1987; MacDowall, 1988; Potter *et al.*, 1990; Neira *et al.*, 1992; Whitfield, 1999).

The distribution and abundance of larvae of estuarine-dependent fishes is largely determined by changes in factors such as river flow, salinity, temperature, depth, dissolved oxygen, estuary morphology, predation, competition and food availability (Whitfield, 1999). In estuarine systems, fishes are generally affected greatly by abiotic factors compared to biotic factors (Baltz *et al.*, 1998; Meng and Matern, 2001; Peterson *et al.*, 2004). One essential adaptation required by fishes that utilise estuaries is the ability to adjust to highly variable salinities and temperatures, two of the main factors responsible for inducing metabolic changes (Dando, 1984; Potter *et al.*, 1990; Whitfield, 1999; Peterson *et al.*, 2004).

For larvae of estuarine-dependent fishes that are spawned in the ocean, another challenge is transport into estuaries, and also maintaining their position inside the estuary. Passive and active mechanisms utilised by larval and juvenile fishes to enter and remain within estuaries have been described in numerous species worldwide (Beckley, 1985; Epifanio, 1988; Whitfield, 1989a; Neira and Potter, 1992a; Kingsford and Suthers, 1996; Forward Jr *et al.*, 1999; Trnski, 2001). These mechanisms are also

related to ontogenetic changes, with early-stage larvae distributing passively by advection and diffusion, and then using vertical migration to avoid outgoing tides as they develop (Melville-Smith *et al.*, 1981; Fortier and Leggett, 1982; de Lafontaine *et al.*, 1984; Tzeng and Wang, 1993; Jenkins and Black, 1994; Harris *et al.*, 1999; Brown *et al.*, 2004; Mao *et al.*, 2004).

1.2 Ichthyoplankton research in temperate Australian estuaries

Most studies on larval fishes in estuaries and enclosed embayments of temperate Australia have been confined to systems in the mainland. These systems include the Nornalup-Walpole Estuary, Swan Estuary, Wilson Inlet and Blackwood River Estuary in Western Australia, Port Phillip Bay, Hopkins River Estuary and Gippsland Lakes in Victoria, and Botany Bay, Lake Macquarie, and Tuggerah Lakes in New South Wales (Lenanton, 1977; Arnott and McKinnon, 1985; Miskiewicz, 1986; Steffe, 1991; Neira and Potter, 1992a,b, 1994; Kingsford and Suthers, 1996; Newton, 1996; Hannan and Williams, 1998; Neira and Sporcic, 2002). In the case of estuaries, most are either temporally closed, shallow or barrier estuaries, with restricted tidal influence and low flow velocities. Seasonality in larval fish concentrations in some of these temperate estuaries and enclosed bays, usually occurs during late-spring/early-summer, with larval fish assemblages dominated by larvae of estuarine species from families such as Gobiidae, Engraulidae and Atherinidae. Unlike temperate systems in mainland Australia, published studies on larval fish ecology in Tasmania are limited to coastal waters or to commercial species such as flathead (*Platycephalus bassensis*) and jackass morwong (*Nemadactylus macropterus*) (Thresher *et al.*, 1989; Jordan *et al.*,

1998; Jordan, 2001a,b,c). The only study on larval fish ecology is a short study at the entrance of the Tamar Estuary (Raudzens, 2002).

1.3 Rationale of this study

The Tamar Estuary is one of the largest estuarine systems in Tasmania that comprises the largest catchment area, and constitutes a major environmental, economic and social asset for the state. However, very little information is available on its hydrology, ecology and biodiversity. The limited information available is based on sparse publications centred on: 1) siltation studies in the upper reaches to address the flooding risks and improving recreational facilities for the city of Launceston (Barrenger *et al.*, 1986; Foster *et al.*, 1986; Hranisavljevic *et al.*, 1994a,b; Sinclair Knight LPH, 1995) and 2) distribution of benthic fauna such as intertidal fauna and foraminiferans and the spread of rice grass along the estuary (Phillips, 1975; Bell, 1996; Smith, 1997).

In addition, the Tamar Estuary is the only mesotidal drowned river valley in Tasmania, and regardless of the increasing levels of environmental degradation and the introduction of two exotic species, *Spartina anglica* and *Crassostrea gigas*, it is considered an estuary with a high conservation significance. Although this category is reserved for estuaries with minimal effects of human activities, the Tamar Estuary was included in this category due to its high plant, invertebrate and fish diversity and because it possesses a large component of species not recorded in any other Tasmanian estuary (Edgar *et al.*, 1999). Despite the importance of the Tamar Estuary as a biodiversity centre, there is a lack of baseline information on how to manage the

estuary's resources as well as ecological data to offer meaningful advice to manage the estuary as a whole ecosystem (ecosystem based management). Consequently, the rationale behind this thesis was to undertake a study that included a very detailed 2-year field study comprising hydrodynamics, larval fishes and zooplankton.

This study comprises the first comprehensive ecological study to be carried out in the Tamar Estuary that incorporates both physical and biological data, and aims to provide information on zooplankton and larval fish dynamics in relation to the hydrodynamics of the estuary. Such information is important for future evaluation of the likely impact(s) of activities such as dredging and fishing in the system, given that alterations in the structure of fish communities in the estuary could be detected from changes in the composition and abundance of larval fishes and, consequently, could be used as biological indicators of changing environmental conditions (Neira and Sporcic, 2002).

1.4 Aims and objectives

Given that the Tamar Estuary is a highly flushed system with strong tidal influence, the following hypothesis was formulated:

The dynamics of larval fishes in a highly flushed estuary like the Tamar Estuary, differ from that exhibited by larval fishes in temperate estuaries subjected to weaker tidal currents.

The aims of the present study were:

- To describe the hydrography of the Tamar Estuary during a one-year cycle, and quantitatively classify the estuary according to its circulation and stratification.
- To describe the temporal and spatial variation of zooplankton biomass along the Tamar Estuary and assess this variation in terms of the environmental conditions.
- To describe the changes in composition and abundance of the larval fish assemblages along the Tamar Estuary, and to examine the effect of environmental factors and zooplankton biomass on the temporal and spatial variation of the assemblages.
- To investigate the influence of tidal currents on larval fishes at the entrance of the estuary, and identify any transport and/or retention mechanisms employed by larvae to remain within the system.

1.5 Thesis structure

Chapter 1 (this chapter) includes a general introduction to the thesis, the rationale, the hypothesis and the specific objectives of the study. Hereafter, the following five chapters are presented as independent papers. This structure may result in a limited degree of repetition, in particular in the introduction, methods and some of the discussion.

Chapter 2 includes a description of the estuary's hydrodynamics and hydrography, with a classification of the estuary according to its circulation and salinity

stratification. Variables obtained during the study period such as temperature, salinity, current velocity, freshwater flow and wind speed and direction are also described.

Chapter 3 describes the seasonal and spatial changes in zooplankton biomass as a proxy for secondary production and a measure of food availability for larval fishes. Both, hydroacoustics using a Doppler current profiler and traditional plankton nets are utilised to estimate zooplankton biomass.

Chapter 4 describes the composition of the larval fish assemblages, as well as seasonal and spatial changes in composition and distribution. These changes are linked to the hydrography and secondary productivity of the estuary.

Chapter 5 describes the influence of tidal and diel phases in larval fish dynamics at the lower Tamar Estuary, through changes in the distribution of the overall concentrations and the dominant families in relation to tides and day light.

Chapter 6 links the hydrodynamics of the estuary and larval fish distribution in the lower Tamar Estuary utilizing a 1-dimensional, simple estuarine transport model to examine transport and retention.

Chapter 7 discusses the results of the entire study and provides general conclusions drawn from the study.

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Chapter 2

Hydrography and circulation of the Tamar Estuary

2.1 Abstract

The hydrographic characteristics and circulation dynamics of the Tamar Estuary are described based on a series of parameters obtained throughout the system between October 2001 and November 2002, and in February 2005. The estuary is a highly flushed system, driven by semi-diurnal tides ranging in amplitude between 3 and 3.5 m from the entrance to the head. Vertical temperature stratification along the estuary was generally weak (<2˚C), and salinity exhibited zero to moderate vertical stratification (~7.1 PSU), the latter recorded in the upper reaches during peak flood season. Mean current velocities recorded with an Acoustic Doppler Current Profiler across three locations in the lower (Ashmans Point), middle (Mowbray Point) and upper (Freshwater Point) regions during February 2005 ranged from 0 to 2 m/s, with flood currents being generally stronger by 0.2-0.4 m/s than ebb currents. Total rainfall (709 mm) and mean freshwater discharge (80.7 m^3/s) were close to the annual average during the sampling period, and winds were predominantly westerly. The Tamar was classified as Type 2a or partially-mixed estuary using freshwater flow, surface current velocity and salinity data. The mean diffusive fraction (ν>0.6) indicates that diffusion (i.e. tidal mixing) accounted for at least 60% of the total upstream salt flux, thereby implying that the estuarine circulation is caused mainly by tidal mixing rather than by gravitational convection. The upper Tamar Estuary region was the only region to change from a Type 2a estuary to a Type 4, or salt wedge estuary, during peak

flooding season, a time when gravitational convection becomes the dominant salt transport process. The weak vertical stratification, together with the strong tidal currents and diffusion driving most of the upstream salt flux in the Tamar, makes this system quite unique among other estuaries in Tasmania.

2.2 Introduction

Physical factors such as river discharge, tidal action, currents, sediment composition, wind and wave energy play an important role in structuring biological communities inhabiting any coastal environment. In estuaries, for example, species composition, distribution of flora and fauna, as well as community interactions at different spatial and temporal scales, are influenced by changes in temperature, type of circulation and related salinity structure (Comim *et al.*, 2004; Mao *et al.*, 2004). To understand how the array of environmental components interact with biological communities at different scales in an ecosystem, it is necessary to have information on the hydrodynamic conditions and on the role these conditions play in the structuring of populations (Officer and Kester, 1991; Morgado *et al.*, 2003).

A number of criteria has been utilized to set up a framework of general principles to classify estuaries which can be used to compare them (Dyer, 1973). These classification criteria include characteristics such as geomorphology, salinity structure, river flow and type of circulation (Dyer, 1973; Ketchum, 1983). One of the schemes that has been widely use to quantitatively compare estuaries is the Hansen and Rattray (1966) classification system, which relies on the ratio of salinity contrast and the ratio of surface velocities and depth average currents (Hansen and Rattray,

1966; Dyer, 1973; Ketchum, 1983; Officer and Kester, 1991; Hunter and Andrewartha, 1992).

The Tamar Estuary is a large highly flushed system with characteristics not found in any other estuary in Tasmania (Edgar *et al.*, 1999). Information on the physical processes that drive the Tamar Estuary is of prime importance to understand the overall ecosystem dynamics, particularly in relation to annual production cycles. While some information on physical characteristics and hydrography is available for this system such as temperature and salinity ranges, size, nutrient loading, chlorophyll a content, etc (Hunter, 1991; Wood, 1992; Pirzl and Coughanowr, 1997; Edgar *et al.*, 1999), the basic properties regarding circulation and mixing processes are poorly understood. The purpose of this chapter is to describe the hydrography and circulation type of the Tamar Estuary, and to classify the estuary according to the circulation and stratification model of Hansen and Rattray (1966).

2.3 Material and methods

2.3.1 Study area

The Tamar Estuary in northern Tasmania is considered a mesotidal drowned river valley, characterized by a winding course which comprises a series of shallow and extensive bays interconnected by channels as narrow as 300 m (e.g. Batman Bridge) (Fig. 2.1). The system has one major navigable channel surrounded by sandbanks and rocky reefs in the lower reaches, and by fine sediment in the upper reaches (Phillips, 1975; Bell, 1996). The bathymetry of the main channel is uneven with depth varying from 2 to 50 m. The shallower regions are usually located in the upper estuary and

wide basins whereas deeper regions are located near the mouth (e.g. Ashmans Pt and Pt Effingham), the middle estuary and narrow channels.

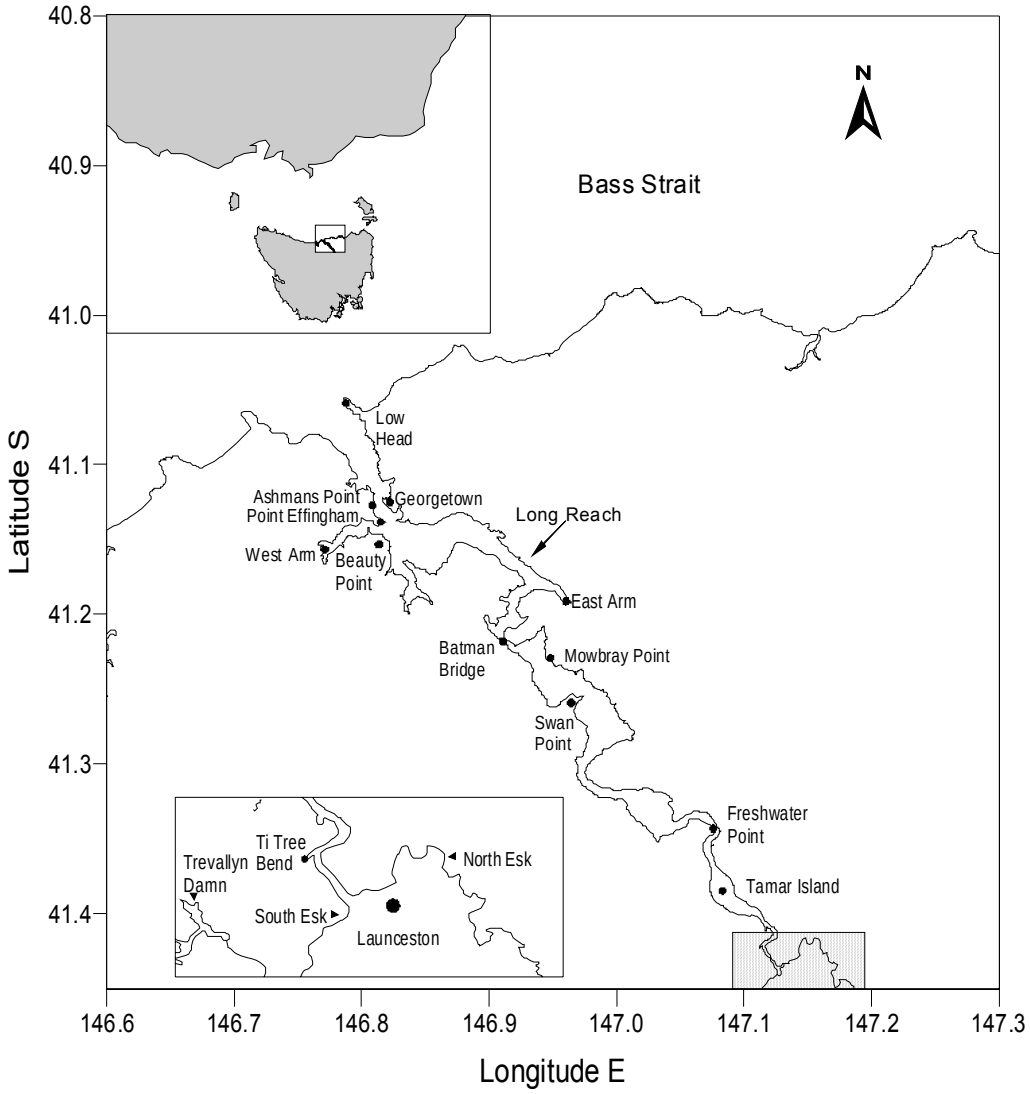

Figure 2.1. Geographical position of the Tamar Estuary in northern Tasmania, showing reference locations where sampling sites were distributed.

Two main tributaries discharge into the estuary, namely the North and South Esk rivers, together draining a catchment area of 11,589 km^2, which is considered the largest catchment area in Tasmania (Edgar *et al.*, 1999). These rivers have moderate and variable runoff levels, and receive annual precipitations of 600-1000 mm over the catchments (Pirzl and Coughanowr, 1997).

The tidal regime is semidiurnal with a moderate diurnal inequality, has an approximately 6-hour flood and 7-hour ebb tide, and a tidal range of 3 m at Georgetown and 3.5 m at Launceston (Phillips, 1975; Pringle, 1982; Bell, 1996). The tidal force, together with the directional changes, constrictions of the estuary's course and uneven bathymetry, generate high velocities that can create large upwellings, whirlpools, turbulence and hydraulic fronts (Wood, 1992). Salinity values at the bottom change gradually from fresh to marine, whereas temperatures have little vertical variation in winter or summer (Bell, 1996; Smith, 1997).

2.3.2 Data collection and processing

To facilitate the analyses, the estuary was arbitrarily divided into three major regions, namely (1) lower estuary, from Low Head to Long Reach; (2) middle estuary, from Long Reach to Swan Pt and (3) upper estuary, from Swan Pt to Tamar Island (Fig. 2.1). Each region was subsequently subdivided into 0.5 nautical miles^2 blocks for random selection of sampling sites. Sampling was divided into "routine sampling" and "24-hour sampling". Routine sampling surveys were carried out monthly between October 2001 and November 2002 at several random sites along the lower and middle estuary. The upper estuary was the only region sampled ~ every second month due to logistical constrains. The 24-hour sampling surveys were carried out during the 2001/2002 summer (December to February) at six fixed sites within the lower estuary throughout an entire day/night ebb and flood tide cycle (Table 2.1).

Vertical profiles of temperature (^{o}C) and salinity (PSU) were obtained at each site with a calibrated Seabird Electronics SBE 19 Conductivity-Temperature-Depth

(CTD) profiler. Current velocity data were recorded during February 2005 using a 600 kHz Acoustic Doppler Current Profiler (ADCP; Workhorse Rio Grande) across Ashmans Point in the lower estuary, Mowbray Point in the middle estuary, and Freshwater Point in the upper estuary (Fig. 2.1). Data were collected across each of the three regions every 45 minutes during an entire tidal cycle (~12 hours) during both neap and spring tides. The ADCP was mounted ~0.3 m below the surface in the port side of a powered aluminium vessel, and data were collected at speeds of 2-3 knots. Bottom tracking from the ADCP was used to control and monitor the boat's speed and heading. The blanking distance and beam angle of the ADCP were set to 0.5 m and 20°, respectively. Data were collected every second in 100 bins each 1 m deep, and processed using the manufacturer's software WinRiver (RD Instruments). Instrument failure did not allow reliable current velocity data to be recorded between October 2001 and November 2002, therefore velocity data used to classified the estuary were collected in February 2005.

Daily rainfall data from nine stations distributed along the estuary, as well as wind velocity data at Low Head, were provided by the Australian Bureau of Meteorology for the period of October 2001 - November 2002. Daily freshwater flow data from Corra Linn and Ballroom stations in the North Esk River were provided by the Australian Bureau of Meteorology and the Department of Primary Industries Water and Environment (DPIWE), respectively, while daily freshwater flow data from the South Esk River were provided by Hydro Tasmania.

Table 2.1. Number of sites sampled during this study in the lower, middle and upper regions of the Tamar Estuary between October 2001 and November 2002. Routine sampling was conducted monthly at random sites distributed along the three main regions. The lower region was sampled on a 24-hour basis during summer months, with sampling surveys conducted at six fixed sites.

	24-hour (lower region)				Routine sampling		
	Flood day	Flood night	Ebb day	Ebb night	Lower	Middle	Upper
Month	CTD	CTD	CTD	CTD	CTD	CTD	CTD
Oct-01	-	-	-	-	7	5	3
Nov-01	-	-	-	-	-	4	3
Dec-01	6	6	6	6	-	4	-
Jan-02	6	6	6	6	-	4	3
Feb-02	6	6	6	6	-	4	-
Mar-02	-	-	-	-	4	4	-
Apr-02	-	-	-	-	4	3	3
May-02	-	-	-	-	4	4	-
Jun-02	-	-	-	-	3	4	4
Jul-02	-	-	-	-	4	4	-
Aug-02	-	-	-	-	4	4	3
Sep-02	-	-	-	-	3	4	-
Oct-02	-	-	-	-	4	3	3
Nov-02	-	-	-	-	3	4	-

2.3.3 Data analyses

2.3.3.1 Hydrography

Temperature and salinity data recorded with the CTD were transformed into text files using the manufacturer's software and cleared of noise. They were subsequently averaged for every site and the profiles plotted using SURFER®. Rainfall data were averaged over all the stations and total fortnightly values estimated and plotted using Sigma Plot®. Freshwater flow data from Corra Linn station in the North Esk, which is the closest to the upper reaches of the Tamar Estuary, were not available from October 2001 to August 2002. However, to complete freshwater flow data from the

North Esk, a linear regression with data from Ballroom station (north of Corra Linn) was used to predict freshwater flow from the North Esk between November 2001 and September 2002. River flow data from October 2001 to November 2002 were then averaged fortnightly for both the North and South Esk rivers. Wind velocity data was plotted seasonally using the software WRPlot.

2.3.3.2 Estuary classification

A series of quantitative parameters were used to classify the Tamar Estuary employing the model of Hansen and Rattray (1966). This classification scheme relies on two dimensionless parameters to determine the partition of upstream salt flux among river discharge, gravitational convection and diffusive modes, namely circulation ($\mathbf{u_s/U_f}$) and stratification ($\mathbf{\delta S/S_o}$). This scheme classifies estuaries into either Type 1 (well mixed), Type 2 (partially-mixed), Type 3 (fjord) or Type 4 (salt wedge) (Hansen and Rattray, 1966; Butler *et al.,* 2000). Gravitational convection refers to the action of gravity upon the density difference between seawater and freshwater and tends to cause vertical salinity stratification, while diffusion refers to external mixing processes such as tidal and wind mixing (Hansen and Rattray, 1966; Butler *et al.,* 2000).

The circulation parameter ($\mathbf{u_s/U_f}$) is defined as the net surface current velocity divided by the integral mean river velocity over a cross-sectional area (**R/A**), where **R** is the mean river discharge and **A** is the cross sectional area. The stratification parameter ($\mathbf{\delta S/S_o}$) is the ratio of the top to bottom salinity difference divided by the mean

salinity over the section. The equations used by Hansen and Rattray (1966) to classify estuaries are:

$$\frac{u}{U_f} = -\frac{\partial \phi}{\partial \eta} \qquad \text{(Eq. 1)}$$

$$\frac{S}{S_o} = 1 + \nu\xi + \frac{\nu}{M}\left[(\eta - 1/2) - 1/2(\eta^2 - 1/3) - \int_0^{\eta} \phi \, d\eta + \int_0^1 \int_0^{\eta} \phi \, d\eta' \, d\eta\right] \qquad \text{(Eq. 2)}$$

and

$$\phi(\eta) = \frac{1}{2}(2 - 3\eta + \eta^3) - \frac{T}{4}(\eta - 2\eta^2 + \eta^3) - \frac{\nu Ra}{48}(\eta - 3\eta^3 + 2\eta^4) \qquad \text{(Eq. 3)}$$

where

u= longitudinal time-mean velocity (m/s)

$\mathbf{u_s}$=longitudinal time mean velocity at the surface, z=0 (m/s)

S= time mean salinity (PSU)

$\mathbf{S_o}$= sectional mean of **S** (PSU)

ϕ= stream function

$\mathbf{U_f}$= integral mean velocity (R/A) (m/s)

R= river discharge rate (m^3/s)

T= dimensionless wind stress

Ra= estuarine Rayleigh number

M= tidal-mixing parameter

ξ= dimensionless horizontal coordinate

η= dimensionless vertical coordinate

ν= diffusive fraction of the total upstream salt flux

A= cross sectional area (m^2)

The river flow velocity ($\mathbf{U_f}$) was calculated from river discharge data from February 2005 (**R**), averaged for the seven days preceding ADCP field trips, and then divided by the average cross-sectional area (**A**) sampled by the ADCP. Surface velocity ($\mathbf{u_s}$) was calculated using the velocity component normal to the transect from the first two depth-cells (first 2 m) of the ADCP, and averaged over the whole tidal cycle and along the transect. Salinity data obtained with the CTD during February 2002 at the same sampling sites were utilized to estimate the stratification parameter ($\mathbf{\delta S/S_o}$). The resultant values of $\mathbf{u_s/U_f}$ and $\mathbf{\delta S/S_o}$ were plotted for comparison with values of the diffusive fraction (calculated for zero wind stress, **T**=0), and with the Hansen and Rattray (1966) estuary types.

2.4 Results

2.4.1 Hydrography

Mean water temperature along the Tamar Estuary during the study period ranged from 11°C during July - August 2002 to 18°C in January - February 2002 (Fig. 2.2a). Temperature showed minimal vertical stratification and a moderate horizontal variation along the system. The maximum difference between surface and bottom temperature (1.2°C) was recorded at the lower estuary in October 2001, while the greatest along estuary variation (4°C) was recorded during July and August 2002 between Bass Strait and Tamar Island (Fig. 2.3; profiles for the whole sampling period are shown in the Appendix A3, A5). The vertical stratification of temperature did not appear to change with either tide, season or location along the estuary (Figs 2.3, 2.5a,b).

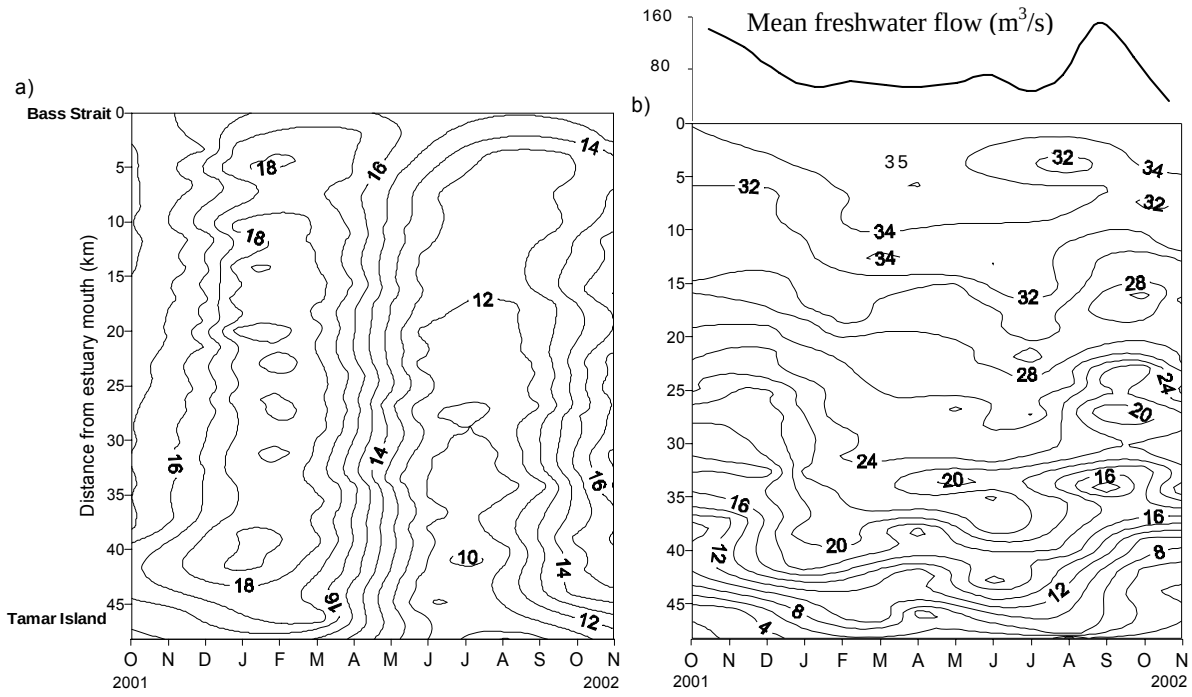

Figure 2.2. Contour plots of depth average a) temperature (°C) and b) salinity (PSU) recorded in the middle of each month along the Tamar Estuary from the entrance at Bass Strait upstream to Tamar Island between October 2001 and November 2002. Mean fortnightly freshwater flow (m^3/s) is shown above the salinity contour.

The temporal variation in salinity was mainly produced by freshwater discharge, which shifted the isohalines up and down the estuary (Fig. 2.2b). Salinity varied gradually from almost zero at the upper reaches to 35 PSU at the mouth, and showed weak vertical stratification during most of the study period (Fig. 2.4). The greatest vertical stratification of salinity (7.1 PSU) was recorded in the upper reaches during peak flood season (Fig. 2.4d), and was also greater during ebb than flood tides (Fig. 2.5c,d).

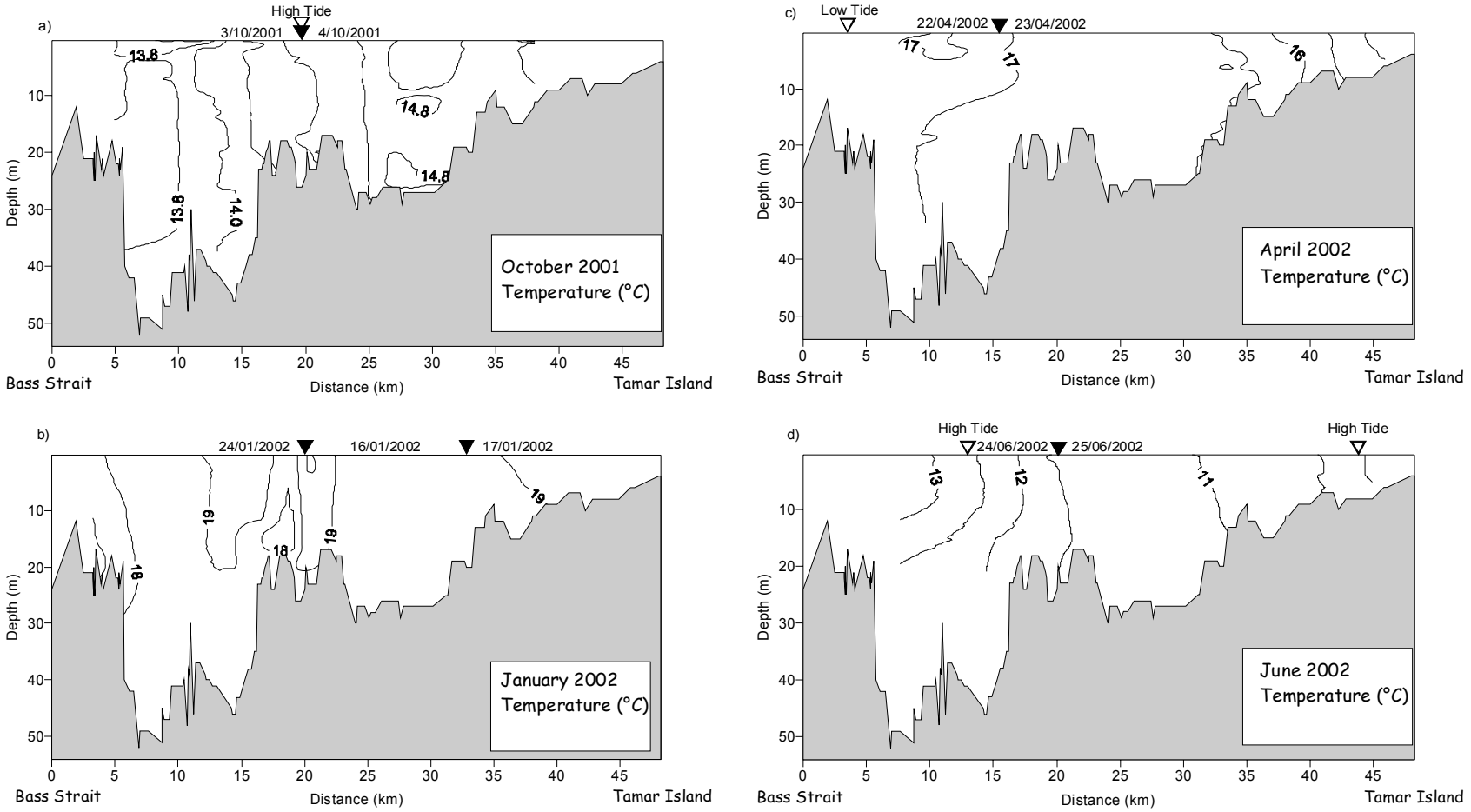

Figure 2.3. Vertical profiles of temperature (°C) along the Tamar Estuary between the entrance at Bass Strait and Tamar Island in a) October 2001, b) January 2002, c) April 2002 and d) June 2002. Black triangles (▼) indicate sections of the estuary sampled on different days, with sampling dates indicated above each section. White triangles (□) indicate the location sampled at high or low tide.

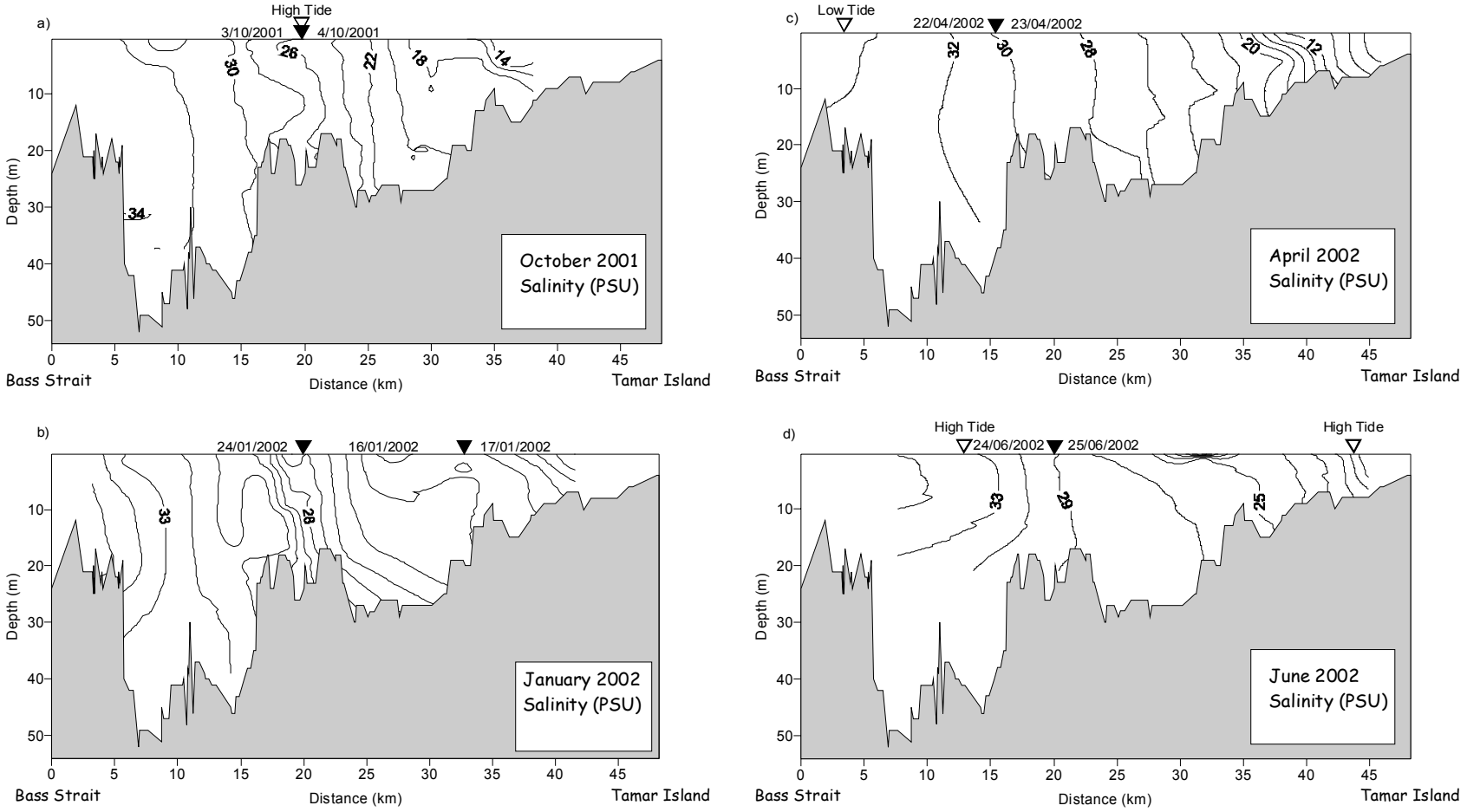

Figure 2.4. Vertical profiles of salinity (PSU) along the Tamar Estuary between the entrance at Bass Strait and Tamar Island in a) October 2001, b) January 2002, c) April 2002 and d) June 2002. Black triangles (▼) indicate sections of the estuary sampled on different days, with sampling dates indicated above each section. White triangles (□) indicate the location sampled at high or low tide.

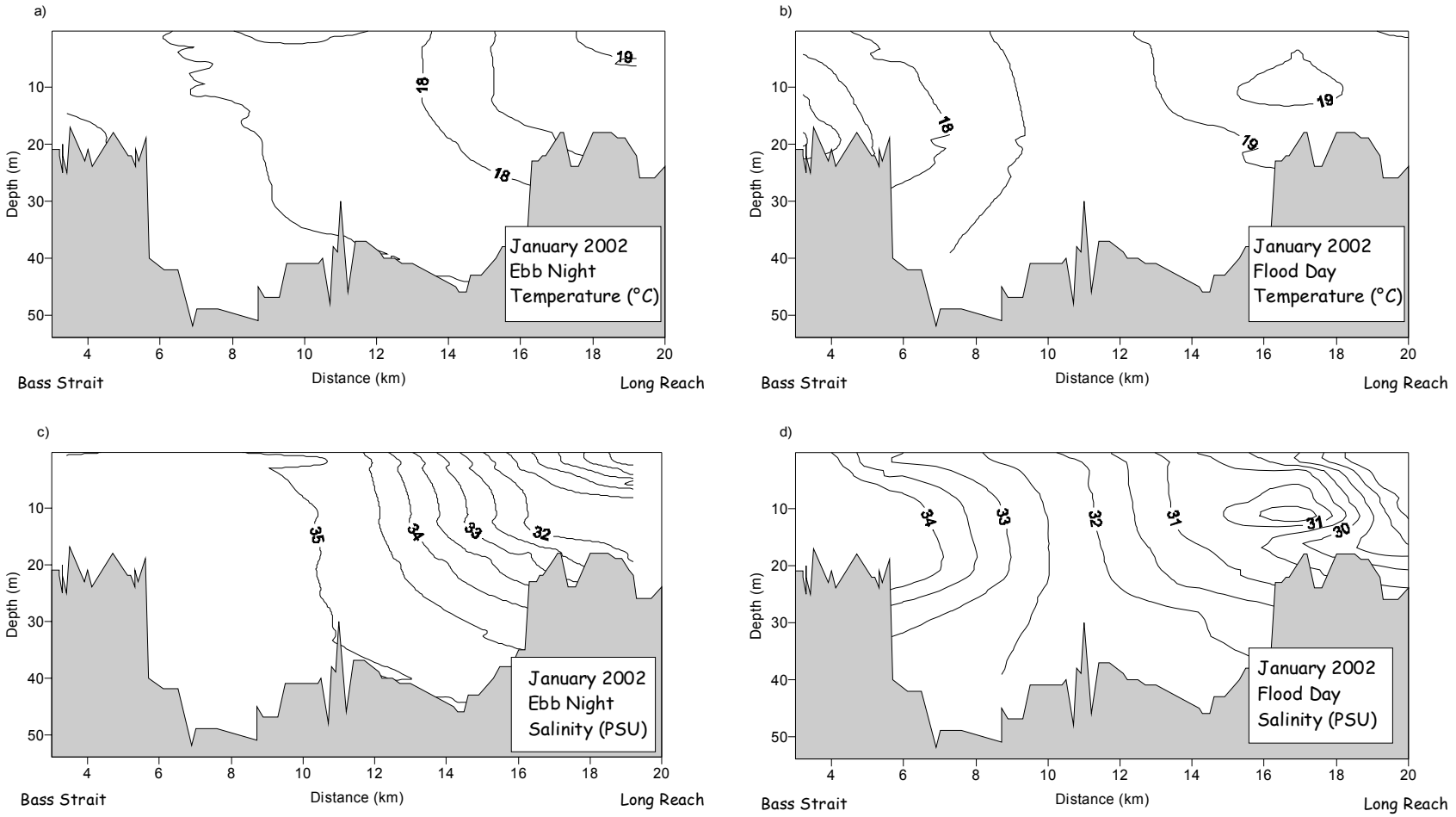

Figure 2.5. Vertical profiles of temperature (°C) in January 2002 during a) ebb night and b) flood day, and salinity (PSU) during c) ebb night and d) flood day along the entrance channel of the Tamar Estuary between Bass Strait and Long Reach.

Current velocities varied with depth and across the different sections of the estuary, and ranged from nearly 0 to 2 m/s during spring tide (Figs 2.6, 2.7). The highest velocities were recorded at Ashmans Pt in the lower estuary and ranged from -2 to 1.2 m/s during peak flood tides, and -0.7 to 1.6 m/s during peak ebb tides, with negative values referring to the upstream current direction (Figs 2.6a, 2.7a). Secondary currents were also recorded along the eastern shore of the estuary. Current velocities at Mowbray Pt and Freshwater Pt in the middle and upper estuary, respectively, also varied with depth and across the estuary, and ranged from -1.2 to 1.0 m/s (Figs 2.6b,c, 2.7b,c). High velocity currents along the estuary were usually recorded at narrow channels such as Batman Bridge (~1.7 m/s), whereas low velocity currents were recorded at wide basins such as that off Swan Point (~0.4 m/s) (Fig. 2.8).

Total fortnightly rainfall along the estuary reached a maximum of 70 mm during October 2002 and decreased to 2 mm during March 2002 (Fig. 2.9a). Maximum freshwater flows were 34 m^3/s from the North Esk during September 2002 and 130 m^3/s from the South Esk during October 2001. The lowest flows recorded were 0.6 m^3/s from the North Esk in April 2002 and 24 m^3/s from the South Esk in November 2002. Freshwater flow contribution from the South Esk was considerably greater than that of the North Esk by an average 56 m^3/s, reaching a maximum of 100 m^3/s during peak flood season (Fig. 2.9b).

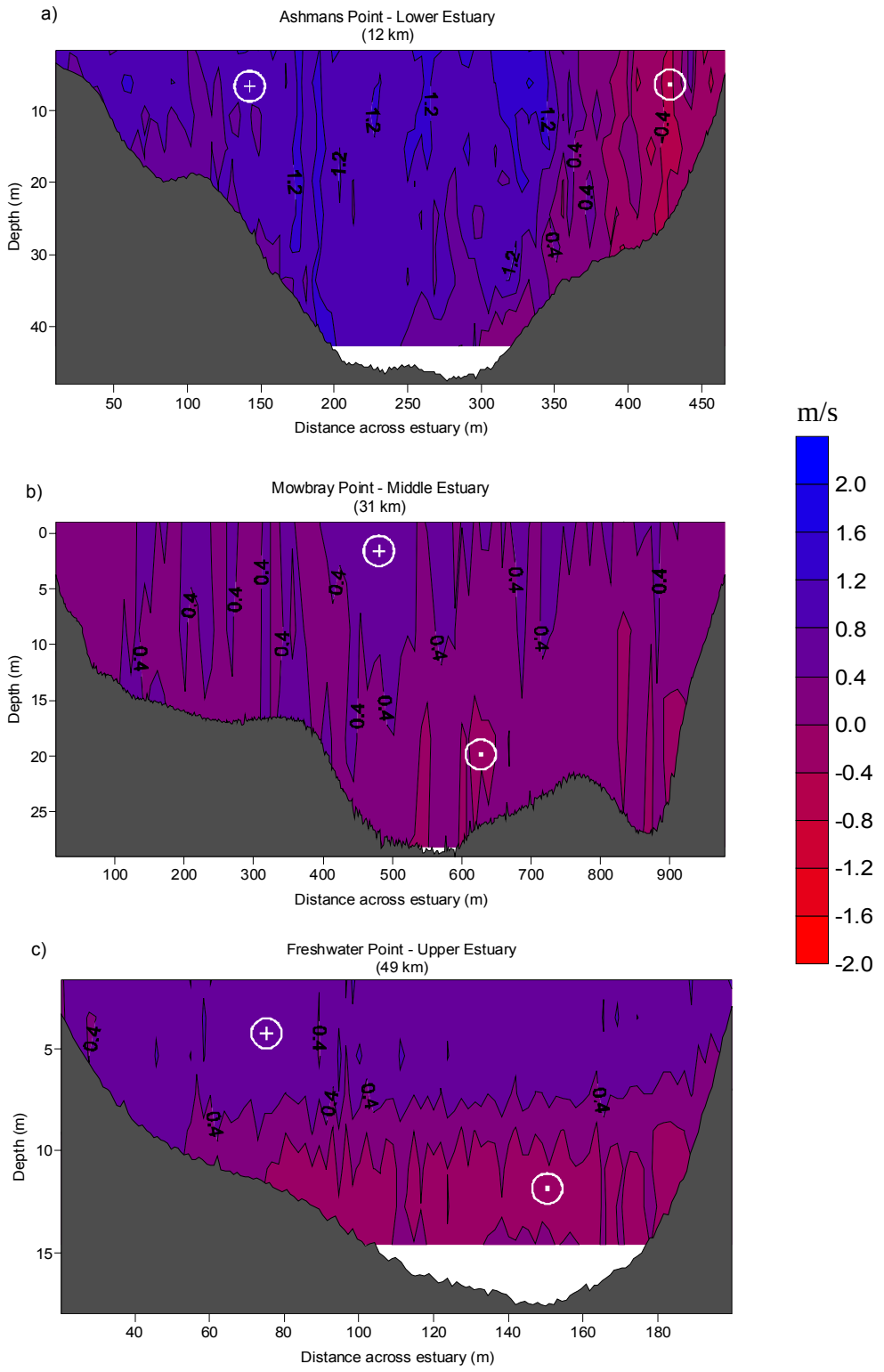

Figure 2.6. Current velocity (m/s) profiles from ADCP data during spring ebb tide across three different sections in Tamar Estuary during 7-9 February 2005. Positive (⊗) and negative (⊙) velocity indicate downstream and upstream currents respectively. Distance from estuary mouth (km) is provided above each profile.

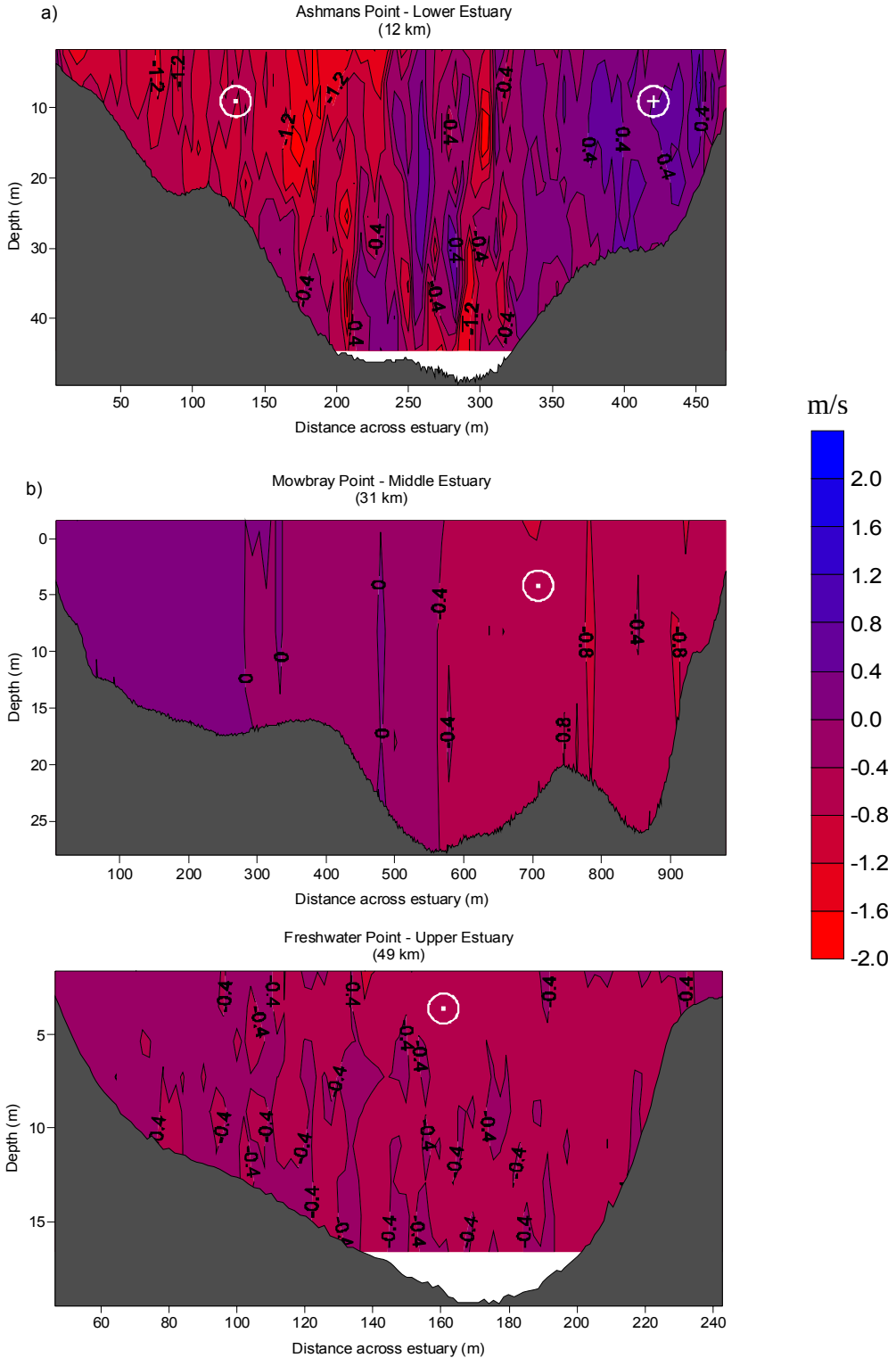

Figure 2.7. Current velocity (m/s) profiles from ADCP data during spring flood tide across three different sections in Tamar Estuary during 7-9 February 2005. Positive (⊗) and negative (⊙) velocity indicate downstream and upstream currents respectively. Distance from estuary mouth (km) is provided above each profile.

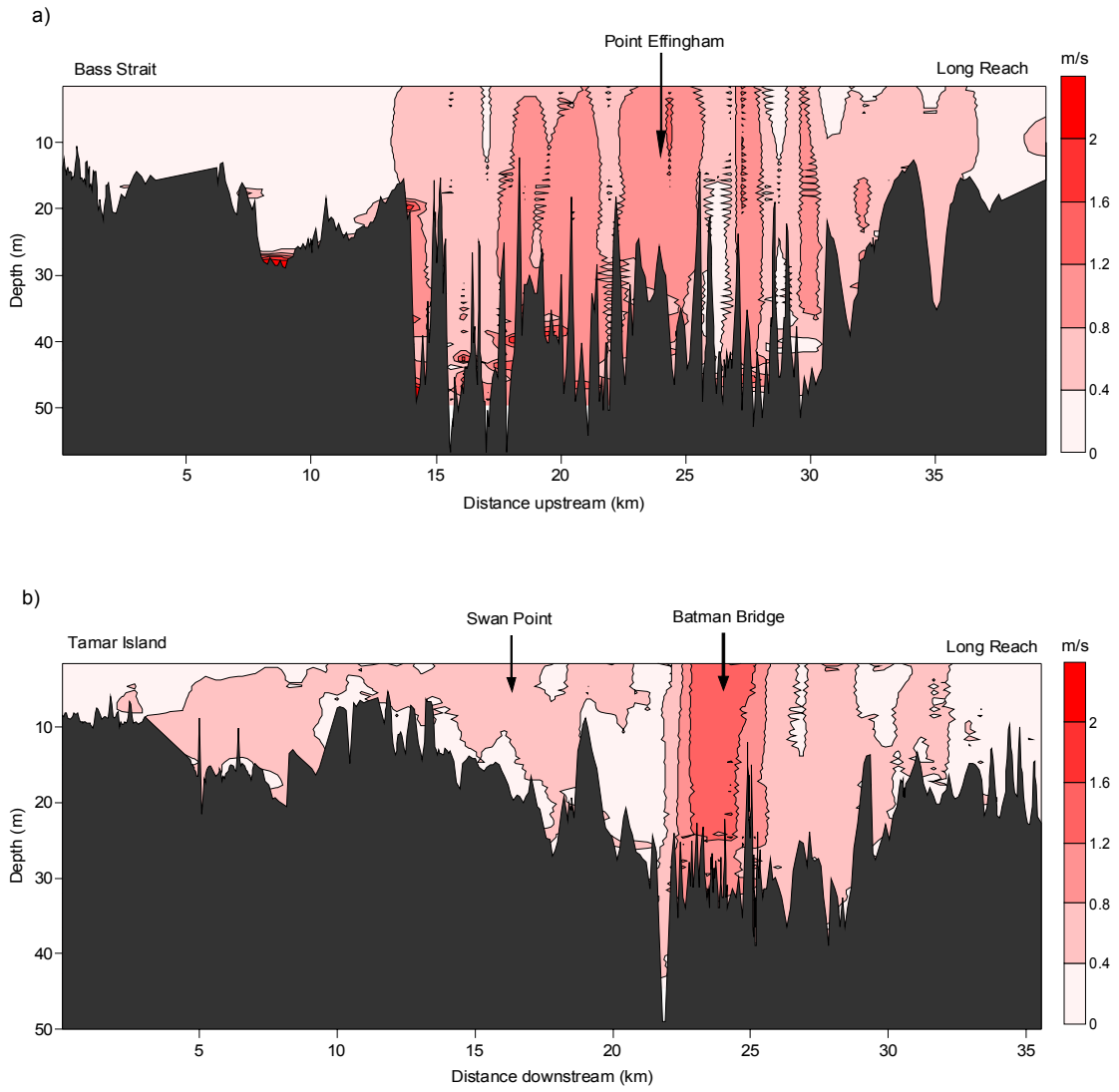

Figure 2.8. Untreated velocity magnitude (m/s) profile during flood tide along the Tamar Estuary in October 2001 recorded by the ADCP. Vessel track in (a) is upstream from Bass Strait to Long Reach and in (b) downstream from Tamar Island to Long Reach.

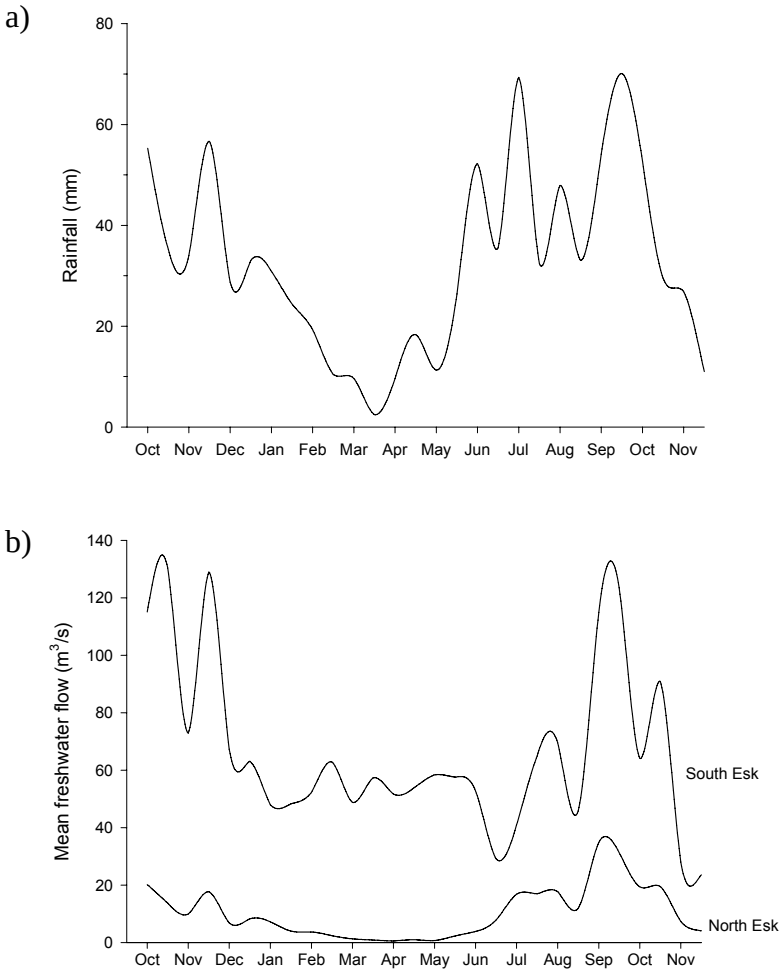

Figure 2.9. Total fortnightly (a) mean rainfall (mm) and (b) mean freshwater flow (m^3/s) in the Tamar Estuary between October 2001 and November 2002. Average daily rainfall from 9 stations located along the estuary were summed every 15 days.

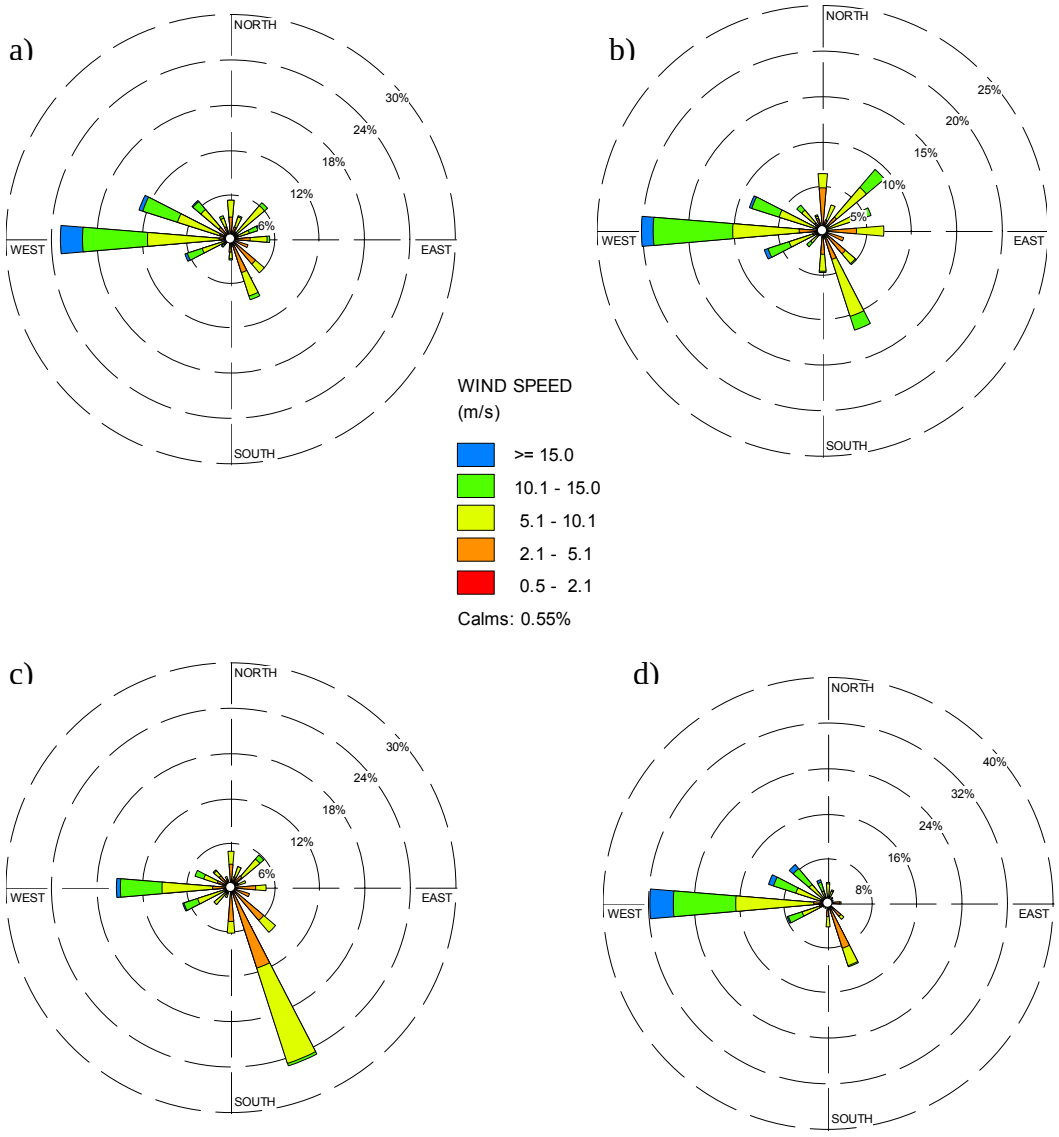

Figure 2.10. Seasonal wind roses showing average winds speed (m/s) and direction from the meteorological stations at Low Head between October 2001 and November 2002. a) Spring, b) Summer, c) Autumn and d) Winter.

Winds were mainly westerlies during spring, summer and winter, turning south-easterlies during autumn (Fig 2.10). Average wind velocities ranged from 0.5 to 20 m/s, with >40% of wind velocities falling in the 5-10 m/s range in all seasons. The percentage of winds with velocities of >15 m/s increased from spring (4 %) to winter (7%).

2.4.2 Classification of the Tamar Estuary

The Tamar Estuary was classified as a Type 2a, or partially-mixed estuary, following the classification model of Hansen and Rattray (1966) (Fig. 2.11). The diffusive fraction (ν) varied from 0.69 to 0.94, with highest values recorded in Freshwater Pt at spring tide, and the lowest in Mowbray Pt at neap tide (Table 2.2). The stratification parameter ($\delta S/S_o$), varied slightly during the year from the region between the entrance and 35 km upstream, whereas sections of the middle and upper estuary >35 km, experienced larger changes in stratification, varying gradually from <0.001 to 0.75 between July and October 2002 (Fig. 2.12). These variations coincided with high freshwater discharge during the same period, which in turn changed the classification of the upper region (Freshwater Pt) from partially-mixed (Type 2a) to salt wedge (Type 4) estuary (Fig. 2.11; red arrow).

Table 2.2. Results from the classification scheme of Hansen and Rattray (1966) for the three different regions in the Tamar Estuary during spring and neap tides. Salinity data used for the stratification parameter was obtained in February 2002 only during flood tide, while velocity data used for the circulation parameter was obtained in February 2005 during a whole tidal cycle at neap and spring tides. AP, Ashmans Pt; MP, Mowbray Pt; FP, Freshwater Pt.

Parameter	**Spring**			**Neap**		
	AP	**MP**	**FP**	**AP**	**MP**	**FP**
Circulation parameter (u_s/U_f)	14.25 ± 2.35	33.20 ± 1.31	7.71 ± 0.43	35.04 ± 2.82	40.95 ± 2.69	4.94± 0.57
Stratification parameter ($\delta S/S_o$)	0.035 ± 0.011	0.038 ± 0.003	0.074 ± 0.002	0.035 ± 0.012	0.038 ± 0.003	0.074 ± 0.002
Diffusive fraction (ν)	0.91 ± 0.01	0.75 ± 0.01	0.90 ± 0.002	0.76 ± 0.02	0.69 ± 0.01	0.94 ± 0.003
Rayleigh number (Ra)	675.8 ± 43.78	2023 ± 38.54	332 ± 8.04	2130 ± 96.06	2731 ± 89.83	176 ± 9.71
Tidal mixing parameter (M)	52.7 ± 6.4	96.7 ± 3.34	12.8 ± 0.25	111.9 ± 14.99	110.3 ± 4.21	8.13 ± 0.33

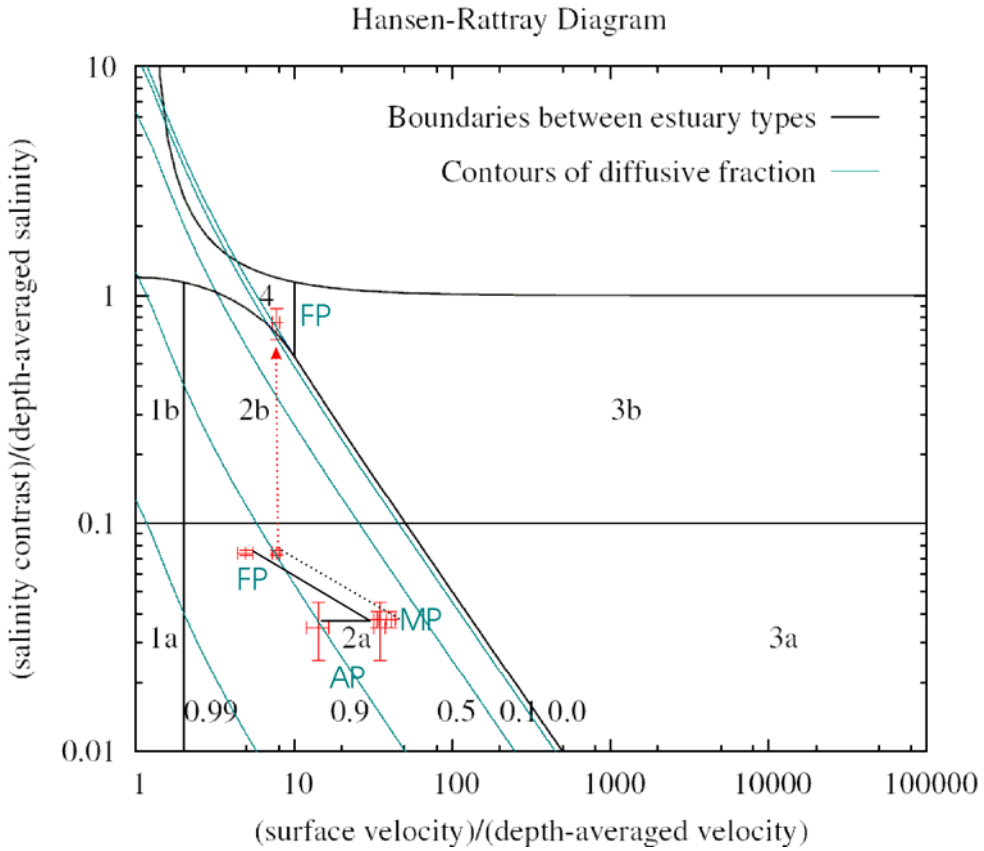

Figure 2.11. Classification of the Tamar Estuary using the Hansen and Rattray (1966) model. The three different regions of the estuary indicated in red, with error bars included, are linked by a black line representing their classification during spring (—) and neap (--) tides for each of the regions. Blue lines represent values of diffusive fraction (ν). Abbreviations: AP = Ashmans Pt; MP = Mowbray Pt; FP = Freshwater Pt, 1 = well mixed; 2 = partially-mixed; 3 = fjord; 4 = salt wedge; "a" and "b" refer to slight or strong stratification respectively. The red dotted line and arrow show the change in the classification of Freshwater Pt from Type 2a to Type 4 estuary in peak flood conditions.

Results from the stratification parameter ($\delta S/S_o$) calculated from data recorded between October 2001 and November 2002 represent the temporal variation of the salinity stratification along the Tamar Estuary at different freshwater discharge levels during that time. Since the ADCP surveys were carried out only at times of low freshwater discharge (summer 2005), it was necessary to asses if the classification of

the estuary changed at peak freshwater discharge. This yielded a change in the classification of Freshwater Pt, which became highly stratified during peak flood conditions and was reclassified from Type 2a to Type 4 estuary (Fig. 2.11).

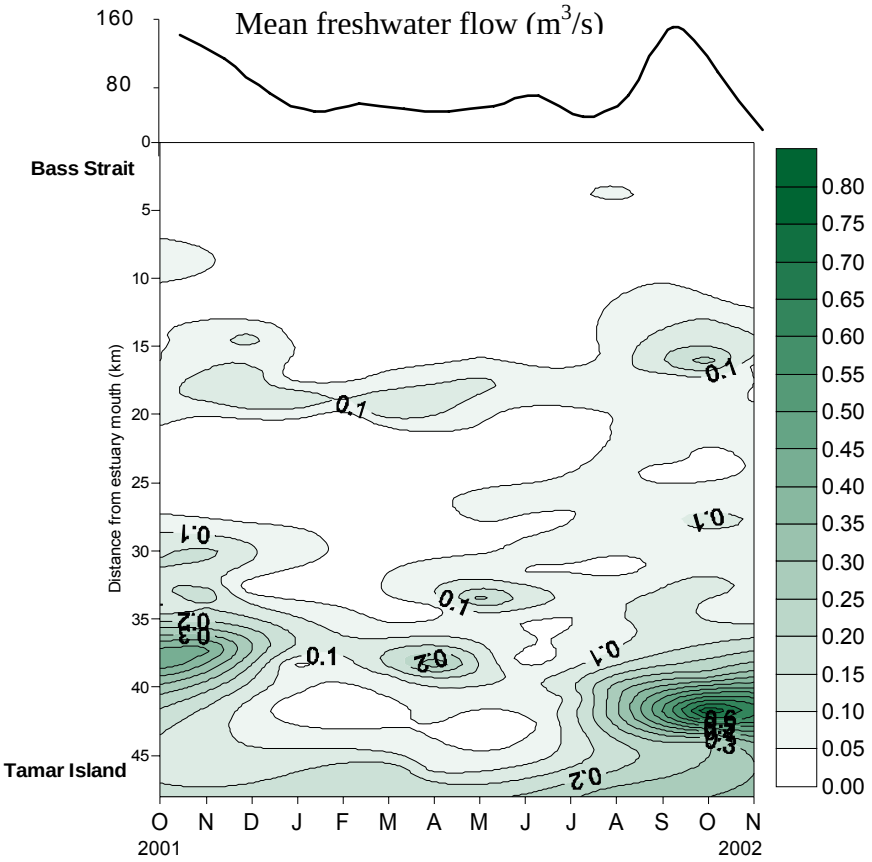

Figure 2.12. Contour of stratification parameter ($\delta S/S_o$) obtained from the salinity data recorded along the Tamar Estuary between October 2001 and November 2002. Mean freshwater flow (m^3/s) from the North and South Esk rivers is provided above the contour.

2.5 Discussion

2.5.1 Hydrography

The extent of the vertical stratification of temperature in the Tamar Estuary was similar to that described in several smaller estuaries in Tasmania, where the difference

between surface and bottom does not exceed 2ºC. However, it was quite different from other major Tasmanian estuaries, such as the Derwent Estuary and Bathurst Harbour, where strong thermal stratification has been observed (Edgar, 1990; Murphy *et al.*, 2003). The weak vertical stratification of the Tamar Estuary compared to the other major Tasmanian estuaries is mainly due to stronger tidal flows that increase vertical mixing and hence the vertical fluxes of water properties such as heat and salt (Phillips, 1975; Pringle, 1982; Simpson *et al.*, 1990; Dyer, 1991; Bell, 1996). As with many other Tasmanian estuaries, the greatest horizontal, along-estuary difference of temperature in the Tamar occurred during winter (~4ºC), with lower temperatures recorded at the upper reaches likely due to colder freshwater runoff (Murphy *et al.*, 2003).

The salinity distribution along the Tamar Estuary varied temporarily in response to freshwater discharge affecting the vertical stratification in the middle and upper estuary, typical of most partially-mixed estuaries (Piccolo and Perillo, 1990). However, while most major estuaries in Tasmania are strongly stratified with salinity differences of >10 PSU between surface and bottom, the Tamar exhibited weak vertical stratification, characteristic of some minor, often shallow, estuaries and other inlets in the state (Edgar, 1990; Coughanowr, 1997; Murphy *et al.*, 2003). In addition, the influence of freshwater discharge in the lower reaches was minimum, and salinity stratification remained weak at all times. Similar to temperature, the weak vertical stratification of salinity is mainly due the turbulent mixing forces generated by the strong tidal motion (Scott, 2004).

Mean current velocities recorded across three sections of the Tamar Estuary indicated that flood currents are stronger than ebb currents by 0.2-0.4 m/s. This difference in current velocities could be due to the slightly longer duration of the ebb flow (7 hours) compared to the flood flow (6 hours), a view that is supported by the fact that a stronger flood flow would be necessary to keep the dynamic balance in the estuary (Mao *et al.*, 2004). Secondary currents found along the eastern side of the estuary at Ashmans Pt are likely due to the bending of the channel to the east. This would enhance the current velocity magnitudes closer to the outer bank (west bank) and produce a weak secondary flow in the inner bank (east bank) flowing in the opposite direction (Dyer, 1973; Perillo, 1996). The opposing currents recorded at Mowbray Pt and Freshwater Pt near the bottom during ebb tides could be due to the estuarine upstream flow being stronger than the ebb flow. Current velocity differences along the estuary were also due to the morphology of the estuary, where higher velocities tend to occur in the narrow, deep channels like Batman Bridge and Ashmans Pt. Maximum current velocity recorded in the Tamar Estuary (2 m/s) was considerably greater than the maximum current velocities reported for the Derwent (0.2 m/s), Huon (0.2 m/s) and Macquarie Harbour (0.25 m/s) estuaries, likely due to smaller tidal ranges (0.8 – 0.9 m) compared to the Tamar (3 m) (Pringle, 1982; Hunter and Andrewartha, 1992; Koehnken, 1996; Butler *et al.*, 2000).

Freshwater inflow responded to rainfall with approximately a one month lag. However, the South Esk River, which contributes to most of the freshwater flow into the estuary, has been dammed for hydro-electricity generation, therefore freshwater inflow from this river is controlled (Pirzl and Coughanowr, 1997).

Along with river flow and tides, winds are recognized as a contributor to circulation and mixing in estuaries (Weisberg and Zheng, 2003). However, it was assumed that the contribution of wind to the Tamar Estuary circulation was small due to much stronger tidal mixing, similar to other partially-mixed estuaries with strong tidal mixing and low wind mixing, such as the Delaware and Yangtze estuaries (Garvine and Whitney, 2006; Lu *et al.*, 2006).

2.5.2 Estuarine classification

Results of this study indicate that the Tamar Estuary is a partially-mixed weakly stratified (Type 2a) estuary, in contrast to estuaries such as the Derwent and Huon (Table 2.3). Both the lower and middle regions of the Tamar are Type 2a, whereas the same regions in the Huon and Derwent are Type 3b (fjord like) and 2b (partially-mixed with moderate stratification), respectively. The upper region of the Tamar Estuary is also Type 2a, although this region changes to Type 4 during peak flood conditions, thus becoming the same type as the upper reaches of Derwent and Huon (Hunter and Andrewartha, 1992; Butler *et al.*, 2000). According to Edgar *et al.* (1999) the Tamar is the second largest estuary in Tasmania, followed by the Derwent, Bathurst and Huon estuaries. In addition, the Tamar Estuary has the largest tidal range and catchment area in the state. These physical features and tidal conditions help explain the unique hydrodynamic characteristics of the Tamar Estuary, compare to other major estuaries in Tasmania.

Current flows in partially-mixed estuaries (Type 2) reverse at depth, and both gravitational convection and diffusion are important contributors to the upstream salt

flux. The distinction of "a" and "b" estuary classes is somewhat arbitrary, but it is convenient to express weak salinity stratification as "a" and medium stratification as "b" (Hansen and Rattray, 1966). However, one of the most important outputs in this classification system is the diffusive fraction (ν), which describes the relative importance of diffusion in relation to gravitational convection. When ν is 1, gravitational convection has a negligible effect on the upstream salt flux, which will be entirely by diffusion. In contrast, as ν approaches 0, diffusion becomes unimportant and the upstream salt flux is dominated by gravitational convection.

Table 2.3. Comparison of physical attributes of the Tamar, Huon and Derwent estuaries according to Edgar *et al.* (1999), and their classification of the lower, middle and upper regions following the Hansen and Rattray (1966) model. Estuarine classes are: 2 = partially-mixed; 3 = fjord; 4 = salt wedge; "a" and "b" refer to slight or strong stratification, respectively. Abbreviations: EDA, estuarine drainage area; ECA, estuarine catchment area.

Region	Tamar	Huon	Derwent
Physical attributes			
Area (km)	98	60	71
EDA (km)	558	311	423
ECA (km)	11,589	3,042	9,255
Tidal range (m)	3	0.8	0.6
Classification			
Lower	2a	3a	2b
Middle	2a	3b	2b
Upper	2a/4	4	4

Values of ν in the Tamar Estuary (0.69-0.94) indicate that >60% of the upstream salt flux is by diffusion, thereby implying that external mixing processes, such as tidal mixing, are more important than gravitational convection. This is particularly true in the upper reaches, where ν values were close to 1 during both neap and spring tides, while the middle and lower reaches were 0.75-0.91during spring and 0.69-0.76 during

neap tides. The difference in ν values between estuary regions is probably due to variation in depth, given that gravitational convection is generally stronger in deeper estuaries, even in the presence of very strong tidal mixing (Hansen, 1967). This supported the fact that Ashmans Pt in the lower estuary and Mowbray Pt in the middle estuary showed lower values of ν than that of Freshwater Pt in the upper estuary.

The Tamar Estuary possesses unique hydrographic and dynamic features which are markedly different from that of other estuaries in Tasmania. While most estuaries are strongly stratified, and gravitational convection plays a major role in the upstream salt flux, salinity transport in the Tamar Estuary appears to be predominantly dominated by diffusion, e.g. tidal mixing. This characteristic is also supported by the lack of strong vertical stratification of both temperature and salinity.

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Chapter 3

Spatial and temporal variation of zooplankton biomass in the Tamar Estuary

3.1 Abstract

The spatial and temporal variability in zooplankton biomass (dry weight) in the Tamar Estuary was assessed between October 2001 and November 2002 using backscatter strength (*Sv*) data from an Acoustic Doppler Current Profiler (ADCP), temperature, salinity and freshwater flow. Biomass was analysed using temperature, and salinity values classified according to the Venice system. Biomass varied temporally but not spatially, and reached peaks in November both in 2001 and 2002, when temperatures were ~15°C. The lack of evident spatial distribution could be due to freshwater flow shifting the boundaries of the Venice salinity regions along the estuary which yielded an unbalanced data set, or to the strong tidal currents which would have been responsible for redistributing zooplankton biomass evenly. Temperature, salinity and freshwater flow explained 49% of the temporal variability in zooplankton biomass. Temperature was the most significant contributor to biomass variability, followed by freshwater flow and salinity. Backscatter strength (dB) was significantly correlated with zooplankton biomass data obtained with nets, and proved to be reasonable indicator that complemented zooplankton surveys, despite the high sediment concentrations characteristic of the middle and upper estuarine regions. The use of ADCP-based backscatter strength as a proxy for zooplankton biomass is also discussed.

3.2 Introduction

The role of zooplankton in estuaries as an essential link between primary producers and higher trophic levels, as well as phytoplankton regulators and nutrient recyclers, is considered by many researchers to be less important than the microbial loop (McLusky, 1981; Sherr *et al.*, 1986; Day *et al.*, 1989; Froneman, 2004). However, estuarine zooplankters play a very important role in transferring energy to higher trophic levels such as fish, shellfish, some crustaceans and other macro-organisms (Reeve, 1975; Capriulo *et al.*, 2002). Their importance lies in the fact that zooplankters graze on a range of available food items, thus making these available to larger consumers (Day *et al.*, 1989). For example, many fish species rely predominantly on zooplankton as their main source of food, particularly at their early larval stages, and interannual fluctuations in adult fish stocks and recruitment success have been linked to availability of planktonic food after the larval yolk supply has been exhausted (Hjort, 1926; May, 1974; Cushing, 1975; Gaughan, 1992; Esteves *et al.*, 2000; Sirois and Dodson, 2000). In addition, peaks in zooplankton biomass in estuaries are closely followed by peaks in larval fish abundances, with subsequent significant declines in zooplankton biomass resulting from intense predation by larval fishes (Thayer *et al.*, 1974; Sherman *et al.*, 1984; Townsend, 1984; Newton, 1996).

Besides standard plankton surveys, hydroacoustic methods have become increasingly more useful in the study of zooplankton distribution patterns and abundance (Flagg and Smith, 1989; Batchelder *et al.*, 1995). Hydroacoustics has the ability to reveal the complex and patchy dynamics of zooplankton in aquatic environments, as well as a variety of biological responses to local physical oceanography, both in temporal and

spatial scales, which have not been possible with traditional sampling methods (Lavery *et al.*, 2002). As a non-invasive technique, hydroacoustic methods are capable of providing real time high-resolution quantitative and qualitative biological data, and are a very potent tool when employed alongside traditional methods (Weeks *et al.*, 1995). In contrast to marine systems, the use of hydroacoustics in estuaries and shallow marine areas has been targeted mostly at sediment dynamics and comparably little on biological processes (Thorne *et al.*, 1991; Hay and Sheng, 1992; Reichel and Nachtnebel, 1994; Gartner, 2004).

The Tamar Estuary is one of the largest, highly flushed, partially-mixed estuarine systems in Tasmania and in temperate Australia (Chapter 2 of this study). Despite being classified as a key ecosystem of high biodiversity in Tasmania (Edgar *et al.*, 1999), there is no information on the zooplankton dynamics, including information on the link between zooplankton biomass and abundance of early stages of fishes. The present chapter examines the temporal and spatial variation of zooplankton biomass and the relationships between zooplankton distribution and environmental parameters such as temperature, salinity and freshwater flow. It also assesses whether backscatter strength data from an Acoustic Doppler Current Profiler (ADCP) could be used as an alternative method to estimate zooplankton biomass. Data on zooplankton abundance and distribution from this chapter is used as a proxy of secondary production and/or food availability for the next chapter.

3.3 Materials and methods

3.3.1 Sampling regime

Sampling throughout the Tamar Estuary was conducted monthly between October 2001 and November 2002. The estuary was arbitrarily divided into three major regions to facilitate comparative analyses between them. These regions are: (1) lower estuary, from Low Head to Long Reach; (2) middle estuary, from Long Reach to Swan Pt, and (3) upper estuary, from Swan Pt to Tamar Island (Fig. 3.1). Each region was subdivided into 0.5 nautical miles^2 blocks from where 8 to 14 sampling sites were selected using a random number generator.

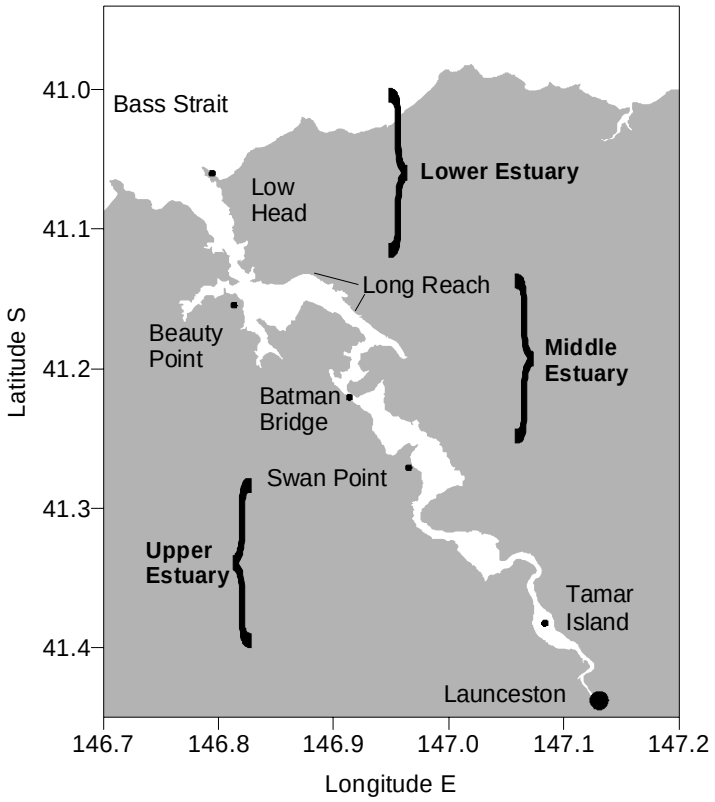

Figure 3.1. Map of the Tamar Estuary in northern Tasmania showing the three main regions sampled during this study.

Zooplankton samples and physical variables were obtained monthly at the selected sites in the lower and middle estuary, and bi-monthly in the upper estuary (Table 3.1). Zooplankton data from the lower estuary is unavailable for November 2001 due to gear malfunction, and between December 2001 and February 2002 due to sampling being concentrated on the larval fish transport component (see Chapter 5 for details).

Table 3.1. Number of sites sampled per month along the Tamar Estuary during this study. Abbreviations: Bio, biological sampling (zooplankton and larval fishes), Env, environmental sampling (CTD and ADCP). Months lacking ADCP data are indicated by *.

	Lower estuary		Middle estuary		Upper estuary		Total number of zooplankton
Month	**Bio**	**Env**	**Bio**	**Env**	**Bio**	**Env**	**samples**
Oct-01	4	7	3	5	3	3	20
Nov-01	Gear malfunction		3	4	3	3	12
Dec-01	Larval fish transport Chapter 5		3	4			6
Jan-02			3	4	3	3	12
Feb-02			2	4			4
Mar-02	3	4	3	4			12
Apr-02	3	4	3	3	3	3	18
May-02*	3	4	3	4			12
Jun-02*	3	3	3	4	3	4	18
Jul-02*	3	4	3	4			12
Aug-02	3	4	3	4	3	3	18
Sep-02	3	3	3	4			12
Oct-02	3	4	3	3	3	3	18
Nov-02	3	3	3	4			12
Total	31	40	41	55	21	22	186

3.3.2 Zooplankton data collection and processing

Replicate samples were collected behind a 14-m steel hull prawn trawler (FTV *Reviresco*) using a bongo sampler equipped with 300 and 500 μm mesh nets, each 3

m in length and 0.6 m in diameter. The sampler was deployed from the stern of the trawler and towed for 10 minutes at a depth of 5-10 m and speeds of 1.0-1.5 knots. Total water volume filtered during each tow (m^3) was calculated from counts obtained from General Oceanics flowmeters attached to the mouth of each net. Samples were fixed on board using 10% formalin-seawater and later preserved in 70% ethanol. The sampling regime yielded a total of 186 samples from 14 survey sessions (Table 3.1).

Larval fishes were removed from both the 300 and 500 μm mesh nets (see Chapter 4 for details). The non fish zooplankton component remaining in the 300 μm net was dried at 40°C for 48 hours in a Contherm Series 5 oven, and later weighed (g) with a Sartorius 1702MP8 electronic analytical balance. Zooplankton biomass was then estimated using water volume filtered and zooplankton dry weight, and standardized to g/100 m^3.

3.3.3 Environmental data collection and processing

Vertical profiles of temperature (^oC) and salinity (PSU) were recorded with a Seabird Electronics SBE 19 Conductivity-Temperature-Depth (CTD) profiler. Downloaded data were transformed into ASCII using the manufacturer's software, and temperature and salinity profiles plotted using SURFER®. Daily data on freshwater flow from Corra Linn Station (North Esk), Trevallyn Pond and Trevallyn Power Station (South Esk) (Fig. 2.1; Chapter 2) were obtained from the Australian Bureau of Meteorology and Hydro Tasmania, respectively, and averaged monthly for analyses. Salinity data from the CTD was used to classify different regions of the estuary according to the Venice System, a system which has been widely used to describe patterns of

distribution of estuarine organisms (Anonymous, 1959; Bulger *et al.*, 1993; Muylaert and Sabbe, 1999; Muylaert *et al.*, 2000; Mouny and Dauvin, 2002; Strydom, 2002). The Venice system was selected for this study in order to ascertain whether zooplankton biomass differed among salinity regions, namely: euhaline (30-36 PSU), polyhaline (18-29 PSU), mesohaline (5-17 PSU) and oligohaline (0.5-4 PSU).

3.3.4 Hydroacoustic data collection and processing

Backscatter strength (dB) was recorded using a 600 kHz Acoustic Doppler Current Profiler (ADCP; Workhorse Rio Grande, RDI). The backscatter strength measured by the ADCP is obtained from the Received Signal Strength Indicator (RSSI) circuit, that has the ability to collect acoustic data approximately every second. These data were recorded simultaneously with zooplankton sampling for later comparison with biomass data obtained with nets. Data were obtained during the period October 2001-April 2002 and August-November 2002, but could not be collected from May to July 2002 due to instrument malfunction (Table 3.1). The ADCP unit was attached to the port side of the vessel and left recording continuously during the entire survey. Data were averaged into 1-minute intervals, with a vertical resolution of 100 bins, each 1 m deep, and processed with TRANSECT (RDI, 2000). The acoustic data from each depth cell was then converted into backscatter strength (*Sv*) using the following modified sonar equation (Deines, 1999):

$$Sv = C + 10\log_{10}[(Tx + 273.16)R^2] - L_{DBM} - P_{DBM} + 2aR + Kc(E - Er) \qquad \text{(Eq. 1)}$$

where:

Sv = backscatter strength (dB)

L_{DBM} = $10\log_{10}$(transmit pulse length) (metres)

$\boldsymbol{P_{DBW}}$ = 10log$_{10}$(transmit power) (Watts)

Tx = temperature of transducer (°C)

R = range along beam (slant range) to scatterers (m)

$\boldsymbol{\alpha}$ = sound absorption coefficient of water (dB m^{-1})

E = echo intensity derived from the RSSI (counts)

Er = echo intensity reference level (counts)

Kc = conversion factor (dB), provided by the manufacturer RDI

C = instrument constant, provided by the manufacturer RDI

Sound absorption coefficient (α) was estimated using CTD data recorded at each site and following the equations of Francois and Garrison (1982a; 1982b):

$$\alpha = \left(\frac{A_1 P_1 f_1 F^2}{f_1^2 + F^2}\right) + \left(\frac{A_2 P_2 f_2 F^2}{f_2^2 + F^2}\right) + \left(A_3 P_3 F^2\right), \text{(dB km}^{-1}\text{)} \qquad \text{(Eq. 2)}$$

where ***F*** = frequency of sound (kHz);

Boric acid contribution:

$$f_1 = 2.8(S/35)^{0.5} \times 10^{(4-1245/\theta)}, \text{(kHz)}$$

$P_1 = 1$

$$A_1 = \frac{8.86}{c} \times 10^{(0.78pH-5)}, \text{(dB km}^{-1}\text{ kHz}^{-1}\text{)}$$

$MgSO_4$ contribution:

$$f_2 = \frac{8.17 \times 10^{(8-1990/\theta)}}{1 + 0.0018(S-35)}, \text{(kHz)}$$

$$P_2 = 1 - 1.37 \times 10^{-4} D + 6.2 \times 10^{-9} D^2$$

$$A_2 = 21.44 \frac{S}{c}(1 + 0.025T), \text{(dB km}^{-1}\text{ kHz}^{-1}\text{)}$$

Pure water contribution:

$$P_3 = 1 - 3.83\times10^{-5} D + 4.9\times10^{-10} D^2$$

$$A_3 = 4.937\times10^{-4} - 2.59\times10^{-5} T + 9.11\times10^{-7} T^2 - 1.50\times10^{-8} T^3 \text{, (dB km}^{-1}\text{ kHz}^{-2}\text{)}$$

where T is temperature (°C), $\theta = 273+T$, S is salinity (ppt), D is depth (m), and c is sound speed (m/s). Pure water contribution is given for T ≤ 20°C.

3.3.5 Data analyses

All statistical analyses were performed using STATISTICA®. Replicate biomass samples (g/100 m^3) were averaged and ln-transformed; zooplankton samples with flowmeter reading errors and/or sample loss were omitted from analyses. One-way ANOVA was performed to test for the temporal variation of zooplankton biomass, while spatial variation was examined only during the period of high zooplankton biomass (October - December 2001, and October and November 2002). Since the number of sites and salinity regions sampled varied monthly yielding an unbalanced data set, one-way ANOVAs were utilized to examine the spatial variation between salinity regions per month. Parametric test assumptions, i.e. normality and homogeneity of variance, were assessed using Cochran's test.

A multiple regression analysis was performed to examine the effect of environmental variables on the distribution of zooplankton biomass in the estuary. Data with a standard deviation ≥3 were regarded as outliers and omitted from the model. Environmental variables were also ln-transformed to obtain normal distribution.

Backscatter strength (*Sv*) data recorded simultaneously with zooplankton sampling were time-averaged for each depth cell. Data from the first two depth cells (1-2 m) were omitted due to noise created by the hull of the vessel. Data from the subsequent 5 m were depth-averaged for comparison with biomass.

A predictive linear regression between zooplankton dry weight and *Sv* was applied to determine whether there was a significant relationship between those variables. A functional linear regression was also performed to correlate *Sv* and zooplankton biomass, as suggested to be appropriate for this purpose (Fielding *et al.*, 2004). The difference between predictive and functional regressions is that the predictive minimizes the sum of the squares of the vertical or horizontal distances from the points to the regression line, whereas the functional measures the central trend of a distribution by minimizing the sum of the products of the vertical and horizontal distance of each point from the line (Ricker, 1973).

To standardize this study with other studies that also employ ADCP backscatter strength, zooplankton dry weight (DW) was divided by 4π. This procedure follows the argument that the target strength, and therefore backscatter strength is $Sv = \mathrm{Log}_{10}(\sigma_s/4\pi)$, where σ_s is the acoustical cross sectional area of the target. Since dry weight is approximately proportional to the cross sectional area of the target and thus to the acoustical cross sectional area (σ_s), the term σ_s can be substituted by dry weight (DW), yielding $Sv = \mathrm{Log}_{10}(DW/4\pi)$ (Flagg and Smith, 1989; Fielding *et al.*, 2004). Because sediment and air bubbles are high sound scatterers (Stanton *et al.*, 1994; Coyle, 2000; Gartner, 2004), data that were deemed to be affected by large sediment

concentrations and air bubbles created by rainfall were discarded from the regression analyses.

Spatio-temporal contours of mean *Sv* along the estuary were created for the whole surveyed area to locate high *Sv* spots and compared them with zooplankton biomass from nets. All contours were created using SURFER®.

3.4 Results

3.4.1 Environmental conditions

Salinity along the estuary during this study ranged from 2.0 to 35.6 PSU, with the lowest salinities recorded during November 2001 and October 2002 in the upper reaches of the estuary. Temporal variation in salinity was evident in the shifting of the boundaries of the Venice regions along the estuary, with the polyhaline (18-29 PSU) and mesohaline (5-17 PSU) regions experiencing most of this shifting. The polyhaline region covered the region between Long Reach (20 km upstream) to Dilston (40 km upstream) during January - June 2002, before retreating downstream from Georgetown (13 km upstream) to Batman Bridge (30 km upstream) during October - November 2002. The mesohaline region extended between Dilston and south of Tamar Island (>45km upstream) during February - July 2002, before shifting downstream from Batman Bridge to Dilston during October - November 2002. The euhaline region (30-36 PSU) remained mostly constant throughout the year, whereas the oligohaline region (0.5-4 PSU) was only detected during October and November both in 2001 and 2002 when it extended north of Tamar Island (Fig. 3.2a,b).

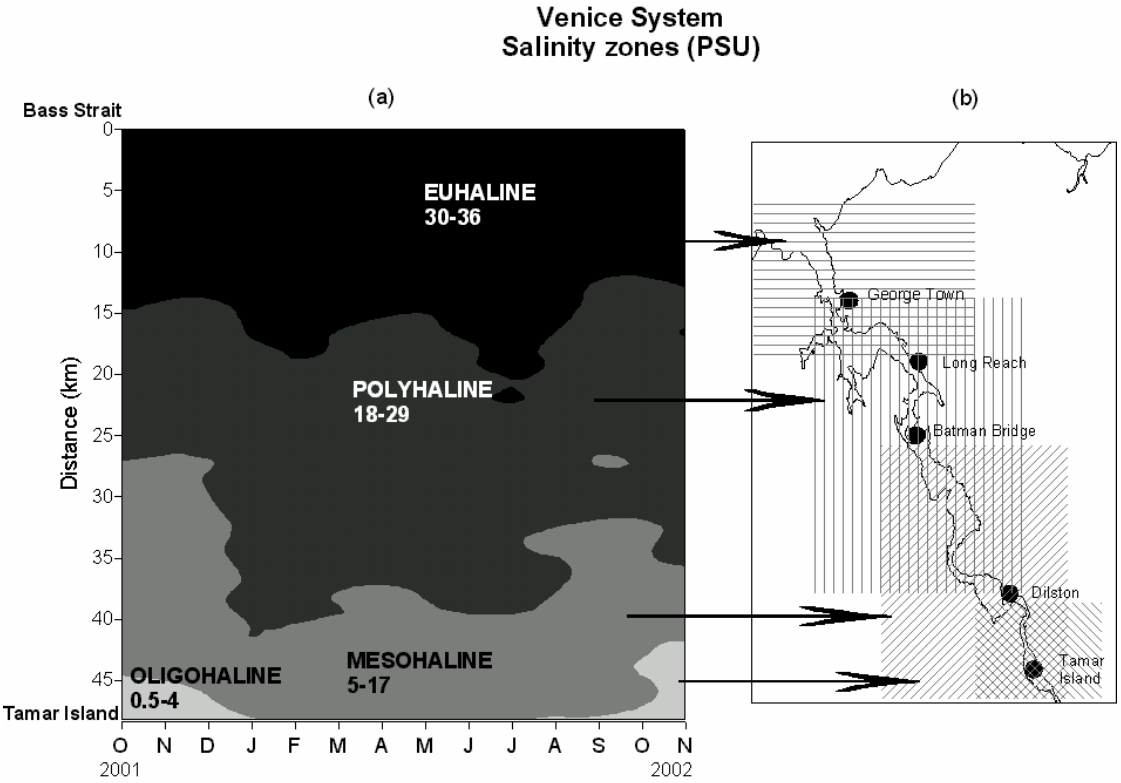

Figure 3.2. (a) Temporal variation of the different Venice salinity regions along the Tamar Estuary between October 2001 and November 2002, and (b) location of the Venice regions. Line patterns in (b) represent the area occupied by the salinity regions in the estuary during the sampling period.

Mean monthly water temperatures throughout the estuary followed a strong seasonal pattern, increasing from 14°C in October 2001 to a peak of 19°C in February 2002 before declining to 11°C in July 2002. Thereafter, temperature started increasing again reaching 16°C in November 2002 (Fig. 3.3a). The highest and lowest freshwater inflow from the South Esk River occurred in November 2001 (123 m^3/s) and June 2002 (41 m^3/s), respectively. By contrast, high and low freshwater inflow from the North Esk River were recorded in September 2002 (33 m^3/s) and April (0.8 m^3/s).

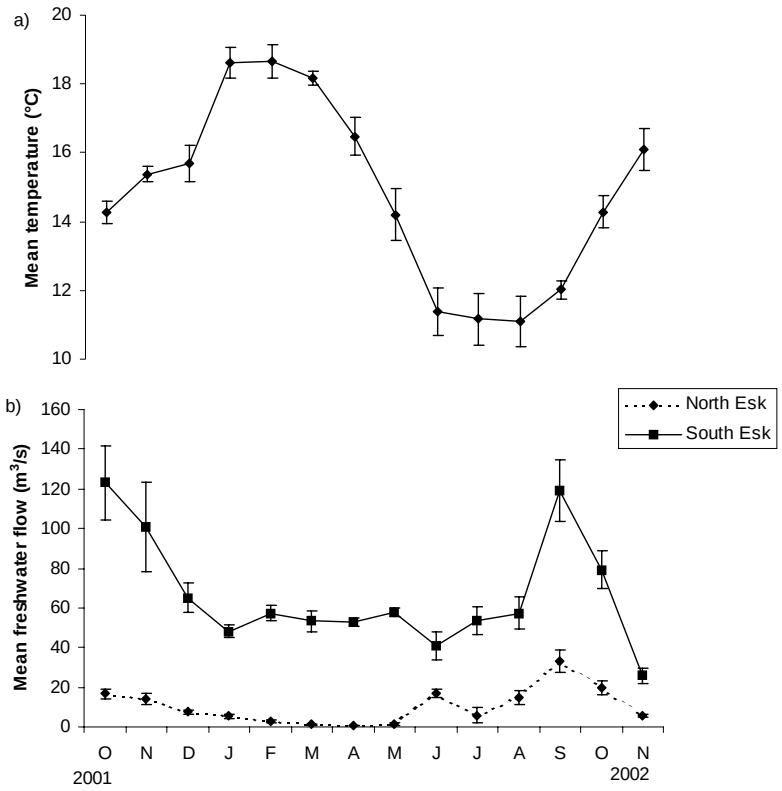

Figure 3.3. Mean (± 95% C.I.) monthly (a) temperature (°C) along the Tamar Estuary, and (b) freshwater flow (m/s) from the North and South Esk rivers between October 2001 and November 2002.

3.4.2 Zooplankton biomass

Mean monthly zooplankton biomass peaked in late spring, November 2001 (4.1 g/100 m^3) and 2002 (1.1 g/100 m^3), when temperatures were ~15°C, and were lowest in winter, July 2002 (0.07 g/100 m^3) (Fig. 3.4, details on statistics in Appendix A7-8).

Mean zooplankton biomass in the euhaline region was highest during October both in 2001 (1.7 g/100 m^3) and 2002 (2.2 g/100 m^3), and lowest during July 2002 (0.1 g/100 m^3) (Fig. 3.5a, details on the statistics in Appendix A9). Biomass peaked in the polyhaline region in November both in 2001 (2.1 g/100 m^3) and 2002 (1.7 g/100 m^3),

and was lowest during July 2002 (0.04 g/100 m^3) (Fig. 3.5b). The highest (6.3 g/100 m^3) and lowest (0.02 g/100 m^3) biomasses in the mesohaline region were obtained in November 2001 and August 2002, respectively, and also corresponded to the highest and lowest values obtained for the overall sampling period (Fig. 3.5c).

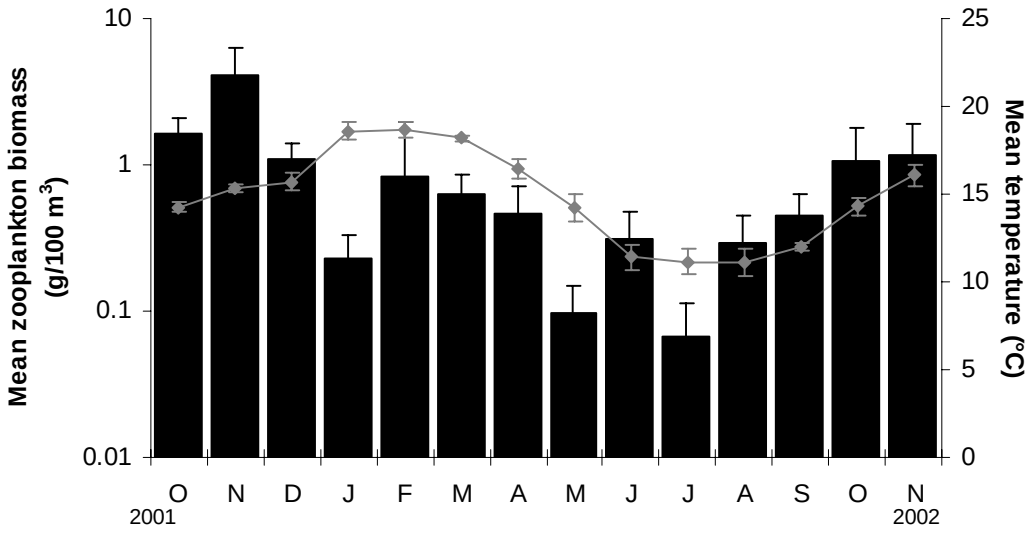

Figure 3.4. Mean (+95% C.I.) monthly zooplankton biomass (g/100 m^3; log-scale) and temperature (°C) in the Tamar Estuary between October 2001 and November 2002.

Table 3.2. Results from one-way ANOVAs (ln-transformed data) for temporal variation of biomass (g/100m^3), and for spatial variation during peak biomass season. NS, not significant; ***P*<0.01. Tukey test abbreviations: E = euhaline; P = polyhaline; M = mesohaline.

	SS	df	MS	F	*P*	Tukey test
Temporal	98.75	11	8.98	9.05	***	
Spatial	SS	df	MS	F	*P*	
Oct 2001	0.08	2.00	0.04	0.10	NS	
Nov 2001	10.46	2.00	5.23	2.19	NS	
Dec 2001	0.10	1.00	0.10	2.41	NS	
Oct 2002	16.15	2.00	8.07	6.51	**	E P M
Nov 2002	0.68	1.00	0.68	4.68	NS	

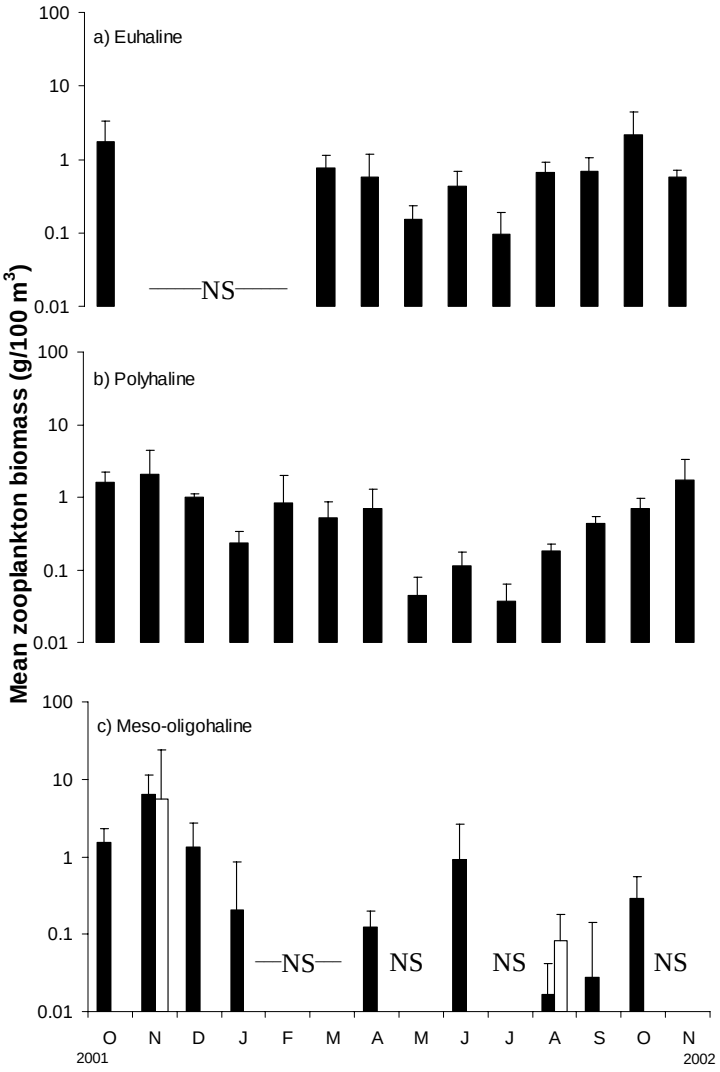

Figure 3.5. Mean (+95% C.I.) monthly zooplankton biomass (g/100 m^3) in the Tamar Estuary at the different Venice salinity regions: a) euhaline, b) polyhaline, c) mesohaline (black bars) and oligohaline (white bars). NS= no samples taken.

Mean monthly zooplankton biomass varied significantly across months (P<0.001) while spatial variation among the three main Venice regions was significant only during October 2002, with a slightly higher biomass in the euhaline than in the mesohaline region (Table 3.2). Lack of spatial variation was also apparent during the other months, when differences between salinity regions were not significant (Fig. 3.6.).

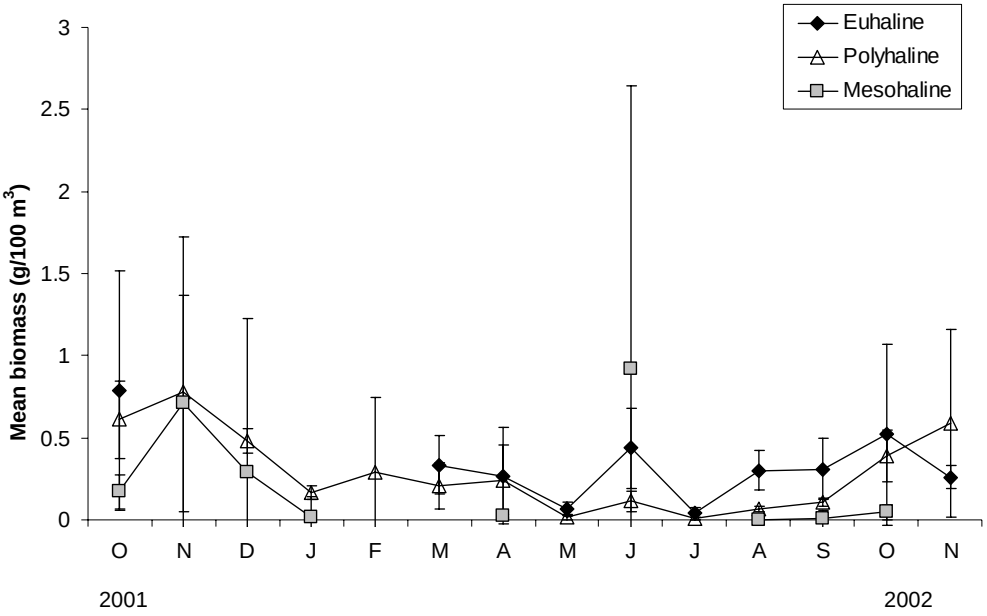

Figure 3.6. Comparison of mean monthly zooplankton biomass (g/100 m^3; ±95% C.I.) between the euhaline, polyhaline and mesohaline regions in the Tamar Estuary during the study period (October 2001 to November 2002).

Multiple linear regression showed that 49% of biomass variability was explained by environmental factors (Table 3.3). Of these, temperature was highly significant (P<0.001), while freshwater flow and salinity were less significant (P<0.05).

Table 3.3. Stepwise multiple linear regression analysis of biomass variability and environmental factors. adjR^2= adjusted correlation coefficient, F= F statistics, Beta= individual standardized regression coefficient, B= raw relation coefficients. *P<0.05; ***P<0.001

R= 0.72	adjR^2= 0.49	F= 22.3		***
		Beta	B	*P*
Month		0.52	0.23	***
Temperature		0.58	0.31	***
Freshwater flow		0.22	0.01	*
Salinity		0.16	0.03	*

3.4.3 Backscatter strength

Backscatter strength (*Sv*) showed a significant linear relationship with zooplankton biomass (R= 0.66, r^2= 0.43, *P*<0.001, n= 71). The resulting equations for the predictive and functional regression fitted to the data as in Figure 3.7 are:

Predictive: ZB = 0.038(Sv) - 0.697

Functional: ZB = 0.058(Sv) + 0.546

Mean backscatter strength (*Sv*) increased with distance from estuary mouth (Fig. 3.8). This increase appeared to be a constant feature, with an increment of almost the same magnitude (~10 dB) between Venice regions, i.e. -80, -70 and -60 dB in the euhaline, polyhaline and meso-oligohaline regions, respectively. Backscatter strength increased with distance from estuary mouth in the euhaline and meso-oligohaline regions but not in the polyhaline region, where it only varied temporarily. The highest *Sv* in the euhaline region was between September and November 2002 (-60 dB), in the polyhaline region during November 2001 (-60 dB), and in the meso-oligohaline region between October and November 2001 (-40 dB).

Backscatter strength did not correspond to zooplankton biomass collected with nets in some months. While the peak in biomass recorded in November 2002 coincided with high *Sv* (-65 to -60 dB), low zooplankton biomass in March 2002 did not match the high *Sv* (-65 to -60 dB) recorded during the same month (Fig. 3.9).

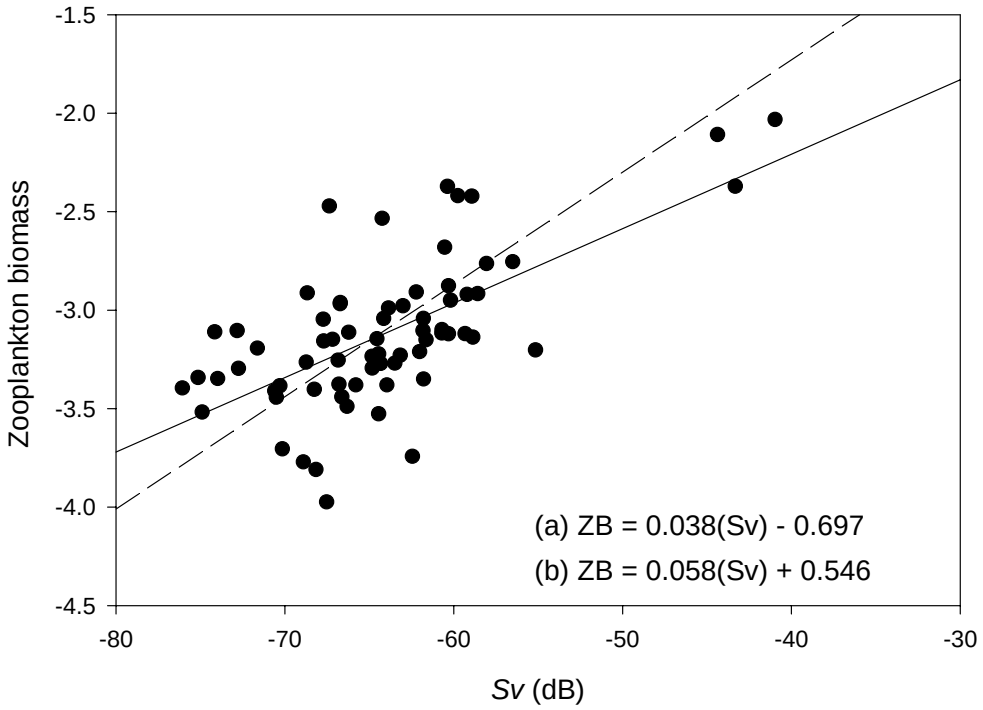

Figure 3.7. Predictive (a,—) and functional (b,---) linear regressions fitted to the relationship between backscatter strength (*Sv*) and zooplankton biomass (ZB = Log[DW/4π]). R= 0.66; r^2=0.43.

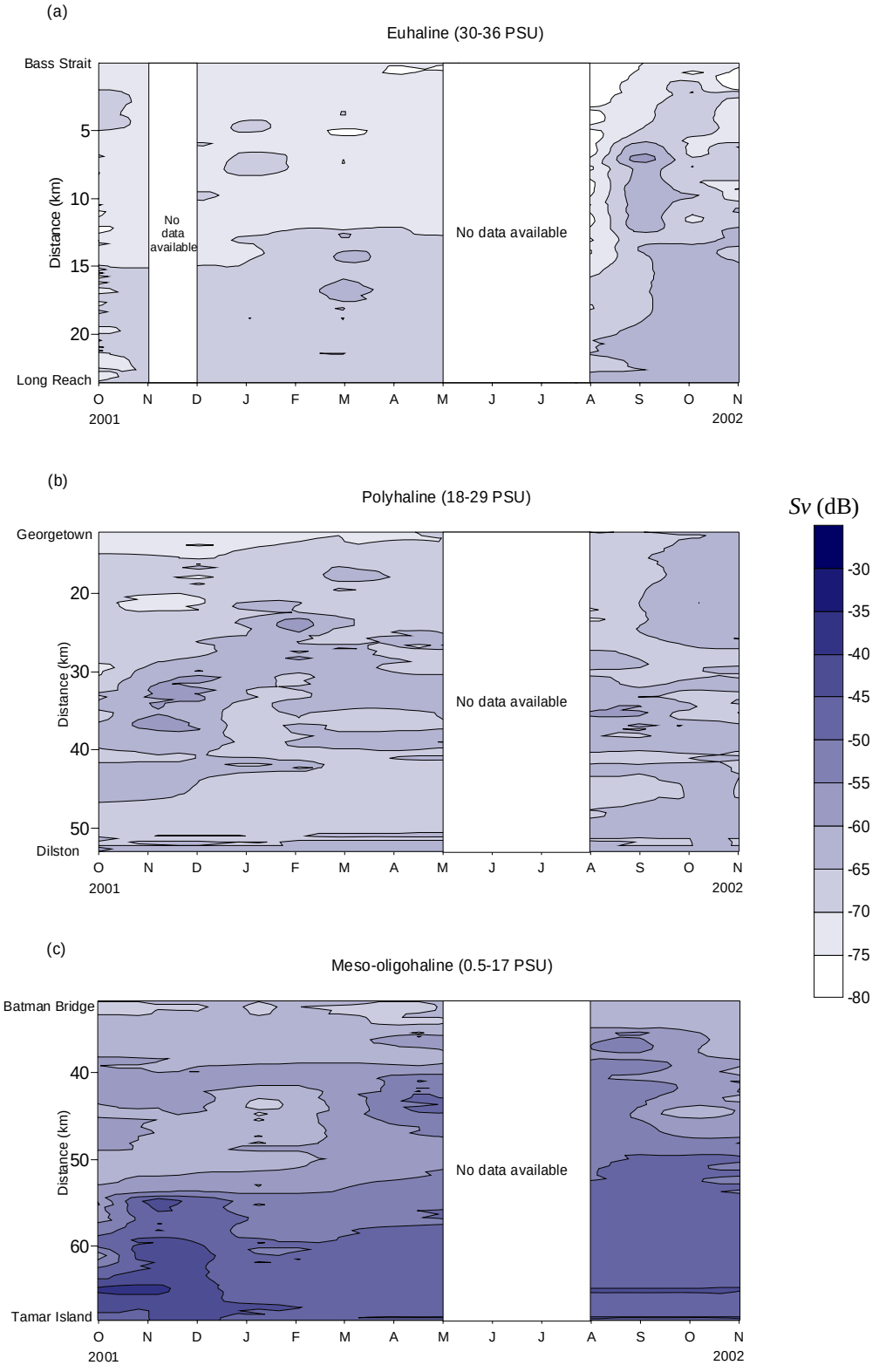

Figure 3.8. Horizontal contours of mean backscatter strength (dB) along the a) euhaline, b) polyhaline and c) meso-oligohaline regions in the Tamar Estuary between October 2001 and November 2002. Data was not available for the period of May - July 2002 due to instrument malfunction.

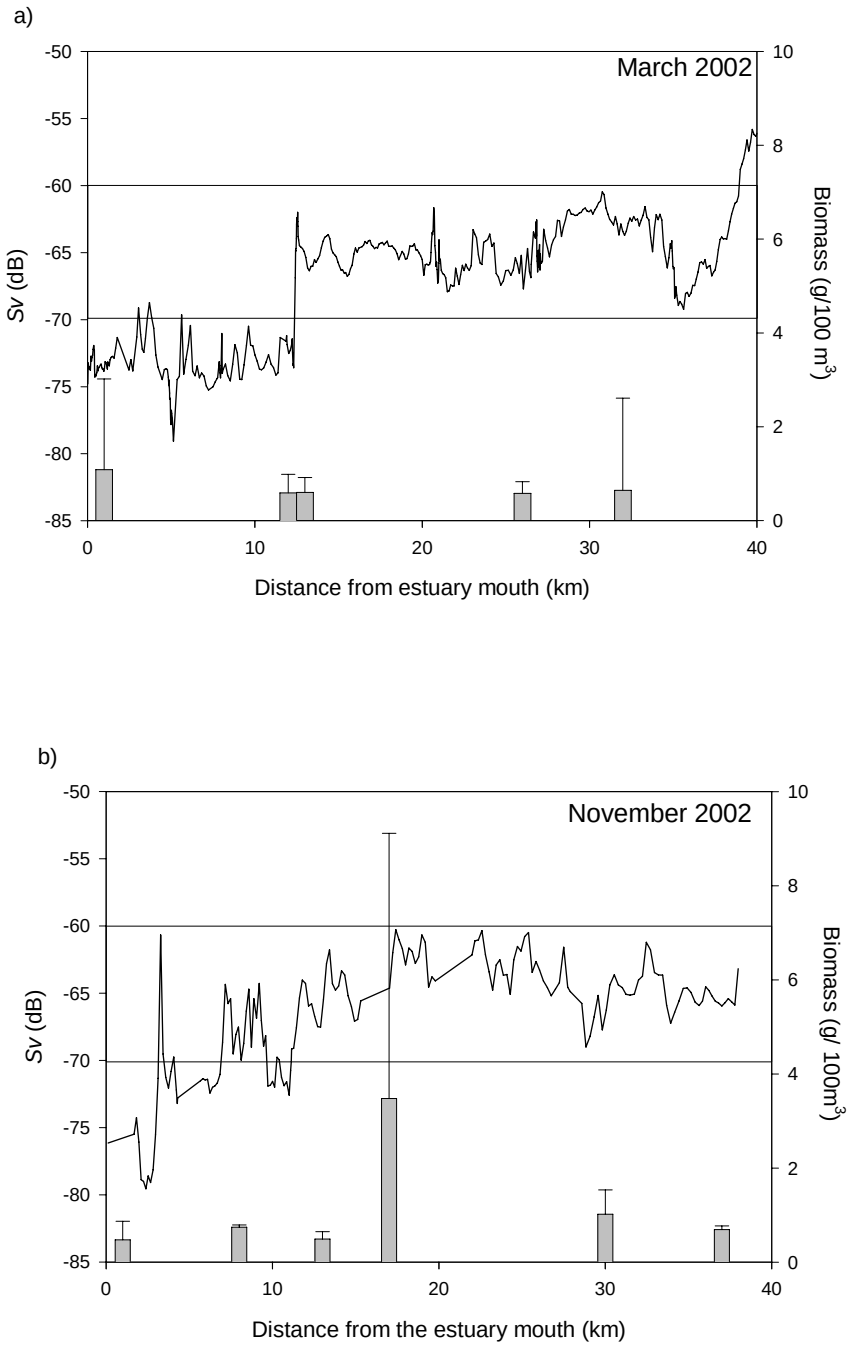

Figure 3.9. Mean *Sv* (dB, solid line) and zooplankton biomass (g/100 m^3; bars) along the Tamar Estuary during a) March 2002 and b) November 2002.

3.5 Discussion

3.5.1 Zooplankton biomass

The late spring (November 2001, 2002) peaks in zooplankton biomass in the Tamar Estuary parallel those described in other zooplankton studies in temperate estuaries in Australia, Europe, North America and South Africa (Sautour and Castel, 1995; Newton, 1996; Capriulo *et al.*, 2002; Mouny and Dauvin, 2002; Froneman, 2004; Roman *et al.*, 2005).

Spatial variation of zooplankton biomass did not differ markedly between Venice salinity regions during the high biomass season (October - December 2001 and October - November 2002). However, this finding contrasts that reported in other temperate systems such as the Seine, Gironde, Ems and Westerschelde estuaries, where higher biomass was recorded in either the mesohaline or the oligohaline region (Sautour and Castel, 1995; Mouny and Dauvin, 2002). Several reasons for the lack of significant spatial difference in zooplankton biomass between salinity regions could be argued: 1) the shifting of the boundaries of the Venice salinity regions leading to an unbalanced data set, 2) strong tidal currents redistributing zooplankton biomass more uniformly along the estuary and/or 3) community composition of zooplankton was not analysed. The unbalanced data set could be an important contributor to this result, as the only region sampled during all months and that extended in most of the sampling area was the polyhaline region, while the euhaline region was not sampled during summer and the mesohaline and oligohaline regions did not extend to the sampling areas during the dry season. In addition, most of the changes in zooplankton distribution along estuaries is closely related to changes in the community

composition and abundance of each of the groups (Sautour and Castel, 1995; Mouny and Dauvin, 2002; Froneman, 2004). Therefore, all three reasons could be the cause for the lack of evident spatial variation in the distribution of zooplankton biomass. Further research that includes extensive sampling across all salinity zones and analyses of community structure is necessary, in order to observed whether spatial differences in the distribution of zooplankton biomass exist and the structure of this distribution.

Changes in temperature, salinity and freshwater flow explained 49% of the temporal variability of zooplankton biomass in the Tamar Estuary, with temperature being the most important contributor. The close relationship between seasonal changes in temperature and zooplankton biomass in the Tamar parallels that described in temperate estuaries in South Africa, North America and Europe (Jerling and Wooldridge, 1991; Sautour and Castel, 1995; Wooldridge, 1999; Froneman, 2001; Capriulo *et al.*, 2002; Mouny and Dauvin, 2002; Roman *et al.*, 2005). The most plausible explanation of this strong link is that metabolic efficiency, growth rate and reproduction of zooplankters are driven mostly by temperature changes (Riley and Conover, 1967; Ketchum, 1983; Day *et al.*, 1989).

In contrast to temperature, salinity showed a weak relationship with zooplankton biomass, both spatially and temporarily. The most likely reason is that salinity has been found to explain mainly spatial variation of plankton distribution at a species level, since the tolerance to the stress caused by salinity is species-specific (Day *et al.*, 1989; Muylaert *et al.*, 2000; Lougee *et al.*, 2002; Mouny and Dauvin, 2002).

Peaks in zooplankton abundance in the Tamar Estuary occurred one month after peak freshwater flows, which usually leads to an increase in nutrients and hence phytoplankton (Wooldridge, 1999; Froneman, 2004). However, multiple regression analyses yielded a weak relationship between fresh water flow and zooplankton biomass variability, possibly due to the presence of numerous environmental factors that may co-vary with fresh water flow and could also trigger a response from organisms (Allanson and Read, 1995; Adams *et al.*, 1999; Wooldridge, 1999; Froneman, 2001; Kimmerer, 2002; Froneman, 2004). Since these factors comprise diverse variables, such as dilution of nutrients and sediments, movements of the salinity fields, residence time and hydrodynamic changes, it is difficult for statistical analyses to distinguish the mechanisms underpinning any particular relationship with freshwater flow (Kimmerer, 2002).

Almost 51% of the variability in zooplankton biomass could not be explained by any of the three environmental factors examined during this study. In this context, it is possible that the November zooplankton biomass peak is related to peaks in chlorophyll *a* recorded in the Tamar Estuary in November (Greg Dowson DPIWE, Tasmania *pers. comm*); following from other estuaries that have reported a strong correlation between chlorophyll *a* and zooplankton abundance (Ketchum, 1983; Froneman, 2001). Factors such as turbidity, physical instabilities and predator presence, have also been reported to affect zooplankton, although they were not considered in this study (Froneman, 2001; North and Houde, 2001; Roman *et al.*, 2001, 2005; Capriulo *et al.*, 2002; Valle-Levinson *et al.*, 2003; Froneman, 2004; Kimmel and Roman, 2004).

Overall results of this study suggest that the influence of the environmental factors examined in the study (i.e. temperature, salinity and freshwater flow) was not as strong as expected. However, these variables were assessed at a biomass level and not community level, where these variables are known to be important in structuring and condition the behaviour of organisms in estuaries (Bain *et al.*, 1988; Thiel *et al.*, 1995; Esteves *et al.*, 2000).

3.5.2 Use of backscatter strength to estimate zooplankton biomass

Results showed that the relationship between log-transformed zooplankton dry weight (DW) and observed backscatter strength (*Sv*) is similar to previous studies, even though those studies were carried out at sea (Batchelder *et al.*, 1995; Zimmerman and Biggs, 1999; Wade and Heywood, 2001; Fielding *et al.*, 2004). High *Sv* areas coincided with areas of high zooplankton biomass obtained from nets on most occasions during this study, except for some regions in March and September 2002 (euhaline), August 2002 (polyhaline) and April 2002 (meso-oligohaline). Intense rainfall and winds exceeding 39 knots during September 2002, as well as the presence of big swarms of large jellyfish clogging the nets during March and April 2002 may have been some of the reasons for this lack of correspondence between zooplankton biomass and *Sv* during those times.

Unlike zooplankton biomass, *Sv* increased steadily with distance from estuary mouth having a difference of ~10 dB between the euhaline, polyhaline and meso-ologohaline regions. This increase in *Sv* was mainly due to an increase in the amount of upstream sediments which may have led to the spread of the data in the regression analyses.

Sediments in the Tamar Estuary vary from marine sediments (sand) between the mouth and Batman Bridge (~30 km upstream) to mud particles (<0.05 mm) occurring between Swan Point and Launceston. The smaller the sediment particle size, the lower their settling velocity and hence the increase of suspended sediments upstream (Foster *et al.*, 1986). However, despite *Sv* being affected by high upstream sediment concentrations, air bubbles and turbulence, the *Sv* from the ADCP complemented zooplankton biomass from nets, particularly during the high zooplankton biomass period. The fact that *Sv* values recorded in the upper estuary during time of high zooplankton abundance were higher than during low abundance regardless of constant sediment concentrations is likely due to the ability of single frequency instruments like the ADCP to detect changes in size over changes in abundance, thus making it easier to detect zooplankton which are larger than sediments (Holliday and Pieper, 1995). Although the objective in the use of ADCP was to detect changes in biomass and not in particle size, the latter could be an advantage in areas with high sediment concentrations like the upper Tamar Estuary. While the combination of hydroacoustic data and zooplankton biomass from nets complement each other in certain conditions, careful attention is still needed when interpreting *Sv* from single frequency instruments (MacLennan and Holliday, 1996; Fielding *et al.*, 2004). Results showed that backscatter strength could potentially be used as a proxy of zooplankton abundance. However, there is still the need to obtained samples for ground truthing and careful attention has to be given to likely sources of noise such as high sediment concentrations, air bubbles and strong turbulent currents.

3.6 References

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Chapter 4

Temporal and spatial variation of larval fish assemblages in the Tamar Estuary

4.1 Abstract

A total of 56,707 larval fishes representing 38 families were collected in monthly surveys carried out throughout the Tamar Estuary between October 2001 and November 2002. The dominant family was the Gobiidae (77.4%), followed by Engraulidae (6.1%), Blenniidae (4.1%), Clinidae (3.7%) and Scorpaenidae (3.3%). Total number of families recorded was highest during spring (35) and lowest (13) in autumn. Number of families decreased with distance from the estuary mouth, with the highest number recorded in the euhaline region (30-36 PSU). Larval fish concentrations followed a clear temporal pattern similar to that of zooplankton biomass, with the highest concentrations occurring during late spring when temperatures were ~ 15°C. By contrast, no significant differences were observed between larval fish concentrations in the different Venice salinity regions. Mean monthly concentrations of all larval fishes peaked during November both in 2001 (270 larvae/100 m^3) and 2002 (381 larvae/100 m^3), and were lowest (0.3 larvae/100 m^3) in June 2002. Gobiid larvae occurred in all months of the study and throughout the estuary and peaked in November 2001 and 2002. Larvae of the anchovy *Engraulis australis* peaked in November 2001 and 2002 and were most abundant between 30 and 40 km upstream from the estuary mouth (polyhaline). Blenniid larvae peaked in December 2001 and November 2002, with higher concentrations between ~10 and 20 km upstream from the estuary mouth (euhaline). Clinid larvae were abundant during several different months, mainly between the entrance channel and 20 km upstream

(euhaline). Two main larval fish assemblages could be distinguished during the peak concentration period, one comprising estuarine spawned larvae and the other, larvae of freshwater species. The spatial variation of the assemblages was closely associated with salinity, which dictated most of the changes in the concentrations of the dominant families and on the assemblage composition. The larval composition, as well as the temporal changes in the larval fish assemblages of the Tamar Estuary, share many of the characteristics typical of other temperate estuaries in Australia and worldwide.

4.2 Introduction

The importance of estuaries worldwide as spawning and nursery areas for fishes has been well documented. Among the reasons that make estuaries ideal areas for many fish species are the abundant food supply, optimal temperatures and lower incidence of predators (Able, 1978; Beckley, 1984; Bell *et al.*, 1984; Powles *et al.*, 1984; Roper, 1986; Potter *et al.*, 1990; Keller *et al.*, 1999; Whitfield, 1999; Strydom *et al.*, 2003).

Four main groups of fishes that utilize estuaries during the larval and juvenile stages could be distinguish according to their life history patterns, namely estuarine residents, marine-estuarine opportunists, marine stragglers and diadromous. Estuarine residents spawn within the estuary, while marine-estuarine opportunists spawn at sea and then migrate into estuaries. Marine stragglers are seldom found in estuaries and they enter these systems infrequently, whereas diadromous species utilize them only

as migratory routes (Beckley, 1985; Lenanton and Potter, 1987; MacDowall, 1988; Potter *et al.*, 1990; Neira *et al.*, 1992; Whitfield, 1999).

The degree to which these groups depend on estuaries varies significantly. Thus, for both estuarine residents and marine-estuarine opportunists, their reliance on estuaries is of prime importance to complete their life cycle, whereas marine stragglers will only enter sporadically mostly to feed (Potter *et al.*, 1990; Neira *et al.*, 1992; Whitfield, 1999). However, most larval fish assemblages in estuaries worldwide are dominated by larvae spawned within these systems, and are characterized by a low diversity and high abundance of some taxa, particularly gobiids and anchovies (Drake and Arias, 1991; Neira *et al.*, 1992; Neira and Potter, 1992a; Whitfield, 1999; Strydom *et al.*, 2003).

Most of the information on larval fishes in temperate estuaries and enclosed bays in mainland Australia originate from temperate systems such as the Swan and Nornalup-Walpole estuaries, Wilson Inlet, Port Phillip Bay, Gippsland Lakes, Botany Bay and Lake Macquarie (Arnott and McKinnon, 1985; Jenkins, 1986; Miskiewicz, 1986; Neira *et al.*, 1992; Neira and Potter, 1992a; Kingsford and Suthers, 1996; Trnski, 2001; Neira and Sporcic, 2002; Trnski, 2002). By contrast, there are no comparable studies of this nature in Tasmanian estuaries. Instead, the few studies on larval fishes in Tasmanian estuaries have been confined to species such as flathead (*Platycephalus bassensis*) and jackass morwong (*Nemadactylus macropterus*), as well as a short study on the ecology of larval fishes at the entrance of the Tamar Estuary (Jordan *et al.*, 1998; Jordan, 2001a,b,c; Raudzens, 2002).

The Tamar Estuary is one of the largest estuaries in Tasmania and is characterized by unique hydrodynamic conditions including strong tidal currents and lack of a two-layered circulation (see chapter 2 for details). Despite being regarded as a key biodiversity ecosystem in northern Tasmania, little information is available on which fish species utilize the Tamar as a spawning/nursery area as well as on larval fish ecology, including composition of larval fish assemblages. The main purpose of this chapter is therefore to describe the composition and abundance of larval fish assemblages within the estuary, and to investigate the influence of environmental factors and zooplankton biomass on the seasonal and spatial variation of the assemblages throughout this system.

4.3 Materials and methods

4.3.1 Field sampling and laboratory analyses

Sampling throughout the Tamar Estuary was conducted monthly between October 2001 and November 2002. The estuary was divided into three major regions from where several sites were selected randomly before each sampling survey (see Chapters 2 and 3 for details). Replicate plankton samples and environmental data were obtained monthly in the lower and middle estuary, and bi-monthly in the upper estuary, mainly during the day at flood tide. In all, 204 plankton samples were obtained from 14 sampling surveys (Table 4.1). Plankton samples were collected with a bongo sampler equipped with 300 and 500 μm mesh nets. The sampler was deployed from the stern of the steel hull FTV *Reviresco* and towed for 10 minutes at depths of 5-10 m. Total water volume filtered during each tow was calculated from

counts obtained with General Oceanics flowmeters attached to the mouth of each net. Samples were fixed in 10% formalin-seawater on board the vessel, and later preserved in 70% ethanol. Larval fish data from the lower estuary in December 2001 to February 2002 correspond to samples obtained during day time flood tides as part of the 24-hr larval transport component of this thesis (see Chapters 5 and 6) (Table 4.1)

Table 4.1. Number of sites sampled, and total number of larval fish samples collected per month along the Tamar Estuary during this study. Abbreviations: Bio, biological sampling (zooplankton and larval fishes); Env, environmental sampling (CTD drops). Months when data originated from daytime samples collected during flood tide in the 24-hour sampling sessions are indicated by * (see Chapter 5 for details).

	Lower estuary		Middle estuary		Upper estuary		Total number of larval
Month/Year	**Bio**	**Env**	**Bio**	**Env**	**Bio**	**Env**	**fish samples**
Oct-01	4	7	3	5	3	3	20
Nov-01			3	4	3	3	12
Dec-01*	3	6	3	4			12
Jan-02*	3	6	3	4	3	3	18
Feb-02*	3	6	2	4			10
Mar-02	3	4	3	4			12
Apr-02	3	4	3	3	3	3	18
May-02	3	4	3	4			12
Jun-02	3	3	3	4	3	4	18
Jul-02	3	4	3	4			12
Aug-02	3	4	3	4	3	3	18
Sep-02	3	3	3	4			12
Oct-02	3	4	3	3	3	3	18
Nov-02	3	3	3	4			12
Total	40	58	41	55	21	22	204

Samples were sorted under a dissecting stereomicroscope and all larval fishes removed, counted and identified to family level. Identifications were carried out using the larval fish guides of Neira *et al.* (1998) and Leis & Carson-Ewart (2000), and the adult fish guide of Gomon *et al.* (1994). Larval fishes that could not be identified to any taxonomic level, i.e. damaged larvae and/or small yolk sac individuals, were

placed under the "unidentified" category. Zooplankton biomass in dry weight was obtained from samples collected in the 300 μm mesh net (see Chapter 3 for details).

Vertical profiles of temperature and salinity were obtained every metre at each site with a calibrated Seabird Electronics SBE 19 Conductivity-Temperature-Depth (CTD) profiler. Freshwater flow data from the North and South Esk rivers were obtained from the Australian Bureau of Meteorology and Hydro Tasmania, respectively (see Chapter 2 for details).

4.3.2 Data analyses

Temperature and salinity data from each site and each sampling month were averaged by depth and mean river flow data was calculated by month. All environmental data were then plotted by month and/or Venice salinity region.

Number of larval fishes from the two plankton nets were added and standardised to concentrations, i.e. numbers per 100 m^3, and replicates then averaged for each site and month. Percentage contribution of families and some individual larval taxa to the total assemblage were calculated using standardized concentrations instead of raw numbers.

All statistical analyses were performed using STATISTICA®. Larval fish concentrations were tested for spatial and temporal variability using ln-transformed data to conform to normality and homogeneity of variance. To test for spatial variations, the Venice System (Anonymous, 1959) was used to divide the estuary into

four different salinity regions, namely euhaline (30-36 PSU), polyhaline (18-29 PSU), mesohaline (5-17 PSU) and oligohaline (0.5-4 PSU). Since temporal variation of larval fish concentrations were clearly evident (Fig. 4.1) and parametric test assumptions to assess this variation were not met, data were analysed only spatially. Spatial variation of overall larval fish concentrations and those of the four most abundant families during peak concentration period (October - December 2001, and October and November 2002) was examined using one-way ANOVA's per month, due to the variation in number of sites and salinity regions sampled monthly, which yielded an unbalanced data set. Parametric test assumptions, i.e. normality and homogeneity of variance, were assessed using Cochran's test. A multiple stepwise regression analysis was performed to examine the effect of environmental factors and zooplankton biomass on the temporal and spatial variation of overall larval fish concentrations and four most abundant families.

Non-parametric multivariate analyses were conducted using PRIMER statistical software to asses spatial variation in the community composition (Clarke, 1993; Warwick, 1993; Clarke, 1999). Concentration data (larvae/100 m^3) per families from the peak spawning periods (October - December 2001 and October and November 2002) were square-root transformed, and a Bray-Curtis similarity matrix generated for all sites sampled during those periods. Families which contributed <0.1% to the total assemblage were omitted from the analyses. Classification and multidimensional scaling (NMDS) ordination were performed to assess relationships between larval fish assemblages in the different sites, followed by an analysis of similarities (ANOSIM) to detect any significant difference between the groups. A SIMPER routine was subsequently applied to determine which key families contributed to the similarity

between groups, and a BIO-ENV analysis to examine the relationships between larval fish assemblages and environmental factors.

4.4 Results

4.4.1 Overall family composition

The 204 samples collected between October 2001 and November 2002 yielded a total of 56,707 larval fishes from 38 families (Table 4.2). Larval fishes from six families accounted for 96% of the total caught during the study (numbers standardised to 100 m^3). Gobiidae was by far the most abundant family, comprising 77.4% of the total number of larvae caught. This was followed by Engraulidae (6.1%), Blenniidae (4.1%), Clinidae (3.7%), Scorpaenidae (3.3%) and Galaxiidae (1.7%). The remaining families (3.6%) each contributed <1% to the total caught. Six families were represented by only one larva, namely Anguillidae, Carapidae, Hemiramphidae, Mugilidae, Pegasidae and Scombridae (Table 4.2).

Total number of families peaked in October 2001 (30) and in October and November 2002 (17), and were lowest in May 2002 (4) (Fig. 4.1d). Overall, 35 families were recorded during spring, while only 13 families were recorded in autumn. Spring, summer and winter were dominated by Gobiidae, which accounted for >60% of the larval fish concentrations, whereas autumn was dominated by larvae of the Galaxiidae (70%) (Fig. 4.2). Total number of families decreased with distance from estuary mouth, with the highest number of families found in the euhaline region (35), followed by the polyhaline (24), mesohaline (12) and oligohaline (7) (Fig. 4.3c,f,i).

Table 4.2. Families and taxa of larval fishes caught along the Tamar Estuary between October 2001 and November 2002, and their respective ranks, abundance, overall percentage contribution and percentage contribution to each salinity region. Families that did not have any species identified were pooled. Ranks are given for each family whose contribution was ≥0.1%. Adjusted numbers correspond to the sum of the monthly numbers of larvae at each site after they were standardized to 100 m^3, and were used to calculate the rankings and percentage contributions. Life-cycle categories are according to Neira & Potter (1994). Abbreviations: Eu, euhaline; Po, polyhaline; Me, mesohaline; Ol, oligohaline; E, estuarine; O, marine estuarine-opportunist; S, marine straggler; F, freshwater.

N	Family / Taxa	Family Rank	Number caught	Adjusted numbers	Percentage of total catch	Eu	Po	Me	Ol	Life-cycle category
1	**Gobiidae**	1	43720	10548.2	77.4	69.1	80.6	79.7	70.9	E, O, S
2	**Engraulidae**	2								
	Engraulis australis		3848	834.7	6.1	0.3	8.5	6.8	0.2	E
3	**Blenniidae**									
	Parablennius tasmanianus	3	2349	555.3	4.1	6.9	3.7	0.3	-	E
4	**Clinidae**	4	2180	509.9	3.7	9.9	2.0	-	-	E, S
5	**Scorpaenidae**	5	1740	444.2	3.3	5.5	2.9	0.5	0.6	S
6	**Galaxiidae**	6								
	Galaxias sp.		36	7.0	<0.1	-	-	0.2	-	F
	Galaxiids		938	231.1	1.7	0.5	0.5	11.1	8.4	F
7	**Gobiesocidae**	7								
	Alabes spp.		76	16.1	0.1	0.4	<0.1	-	-	S
	Gobiesocids.		315	83.2	0.6	2.0	0.2	-	-	S
8	**Tripterygiidae**	8	314	64.9	0.5	1.1	0.3	-	-	S
9	**Bovichtidae**	9								
	Bovichtus angustifrons		10	2.5	<0.1	<0.1	<0.1	-	-	S
	Pseudaphritis urvilli		129	51.0	0.4	0.2	0.1	-	14.7	E
10	**Pleuronectidae**	10								
	Ammotretis rostratus		23	6.3	<0.1	0.1	<0.1	0.2	-	E
	Rhombosolea tapirina		161	45.6	0.3	0.8	0.2	0.2	-	E
	Pleuronectids		2	0.4	<0.1	-	<0.1	-	-	
11	**Tetraodontidae**	11	161	36.4	0.3	0.1	0.4	0.2	-	S
12	**Retropinnidae**	12								
	Retropinna sp.		102	26.4	0.2	-	0.1	0.4	5.1	F
13	**Odacidae**	13	83	21.8	0.2	0.5	0.1	-	-	S, O
14	**Monacanthidae**	14								
	Brachalutheres jacksonianus		20	5.3	<0.1	0.1	<0.1	-	-	S
	Monacanthids		70	16.0	0.1	0.3	0.1	-	-	S
15	**Syngnathidae**	15	46	12.7	<0.1	0.2	0.1	-	-	E, S
16	**Leptoscopidae**	16	34	9.4	<0.1	0.2	<0.1	-	-	S
17	**Platycephalidae**									
	Platycephalus bassensis		28	8.1	<0.1	0.2	<0.1	<0.1	-	E

Table 4.2. *Continued*

N	Family / Taxa	Family Rank	Number caught	Adjusted numbers†	Percentage of total catch	E	P	M	O	Life-cycle category
18	**Labridae**		21	5.1	<0.1	0.1	<0.1	-	-	S
19	**Gempylidae**									
	Thyrsites atun		15	5.1	<0.1	0.1	-	-	-	S
20	**Myctophidae**		16	4.7	<0.1	0.1	<0.1	-	-	S
21	**Pomacentridae**									
	Parma sp.		4	1.1	<0.1	<0.1	<0.1	-	-	S
	Pomacentrids		21	4.4	<0.1	0.1	<0.1	-	-	S
22	**Callionymidae**		14	4.3	<0.1	0.1	<0.1	-	-	S
23	**Triglidae**		16	4.1	<0.1	0.1	-	-	-	S
24	**Gonorhynchidae**		12	3.7	<0.1	0.1	<0.1	-	-	S
25	**Serranidae**		11	3.3	<0.1	0.1	<0.1	-	-	S
26	**Atherinidae**		15	2.8	<0.1	<0.1	<0.1	-	-	E
27	**Moridae**									
	Pseudophycis sp.		1	0.3	<0.1	<0.1		-	-	S
	Morids		8	2.4	<0.1	0.1		-	-	S
28	**Cynoglossidae**		4	1.2	<0.1	<0.1	<0.1	-	-	S
29	**Pempheridae**		3	1.0	<0.1	<0.1	-	-	-	S
30	**Creediidae**		3	1.0	<0.1	<0.1	-	-	-	E
31	**Clupeidae**									
	Sardinops sagax		3	0.7	<0.1	-	-	<0.1	-	S
	Sprattus novaehollandiae		1	0.4	<0.1	-	-	-	0.2	S
	Clupeids		1	0.2	<0.1	-	<0.1	-	-	S
32	**Centrolophidae**									
	Seriolella brama		2	0.6	<0.1	<0.1	-	-	-	O
33	**Anguillidae**		1	0.2	<0.1	-	-	<0.1	-	F
34	**Carapidae**		1	0.3	<0.1	<0.1		-	-	S
35	**Hemiramphidae**		1	0.4	<0.1	<0.1	-	-	-	E
36	**Mugilidae**									
	Aldrichetta forsteri		1	0.2	<0.1	-	-	<0.1	-	O
37	**Pegasidae**		1	0.2	<0.1		<0.1	-	-	S
38	**Scombridae**									
	Scomber australasicus		1	0.4	<0.1	<0.1	-	-	-	S
	Unidentified		145	39.4	0.3	0.6	0.2	0.3	-	
	Total		56707	13623.7						

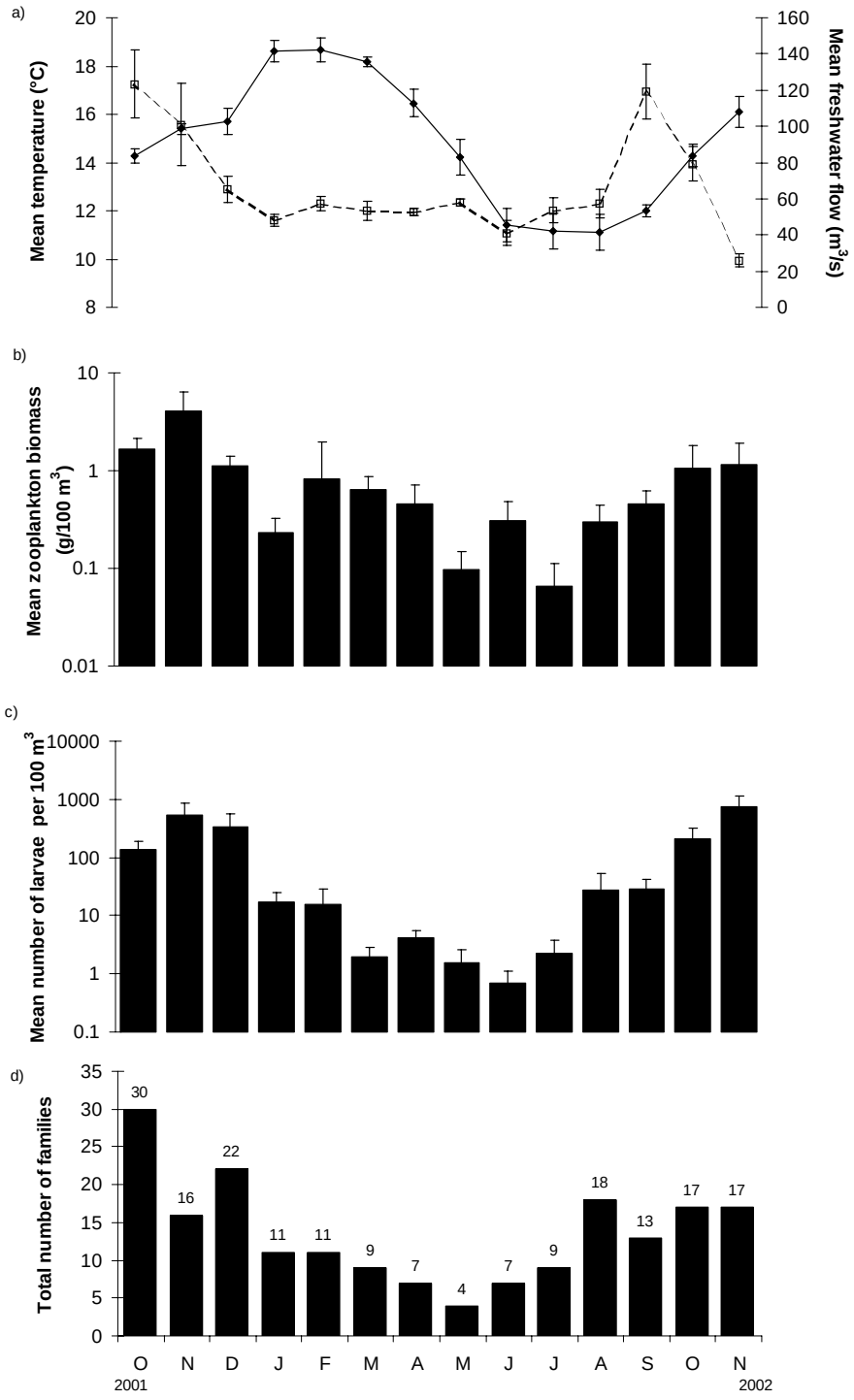

Figure 4.1. Mean monthly (± 95% C.I.) a) temperature (°C, —), b) zooplankton biomass (g/100 m^3), c) concentrations of larval fishes (larvae/ 100 m^3, log-scale) and d) total number of families in the Tamar Estuary between October 2001 and November 2002. Values above bars in d) correspond to the total number of families. The mean monthly (± 95% C.I.) freshwater flow (m^3/s) from the South Esk River (---) is shown with mean temperatures in (a).

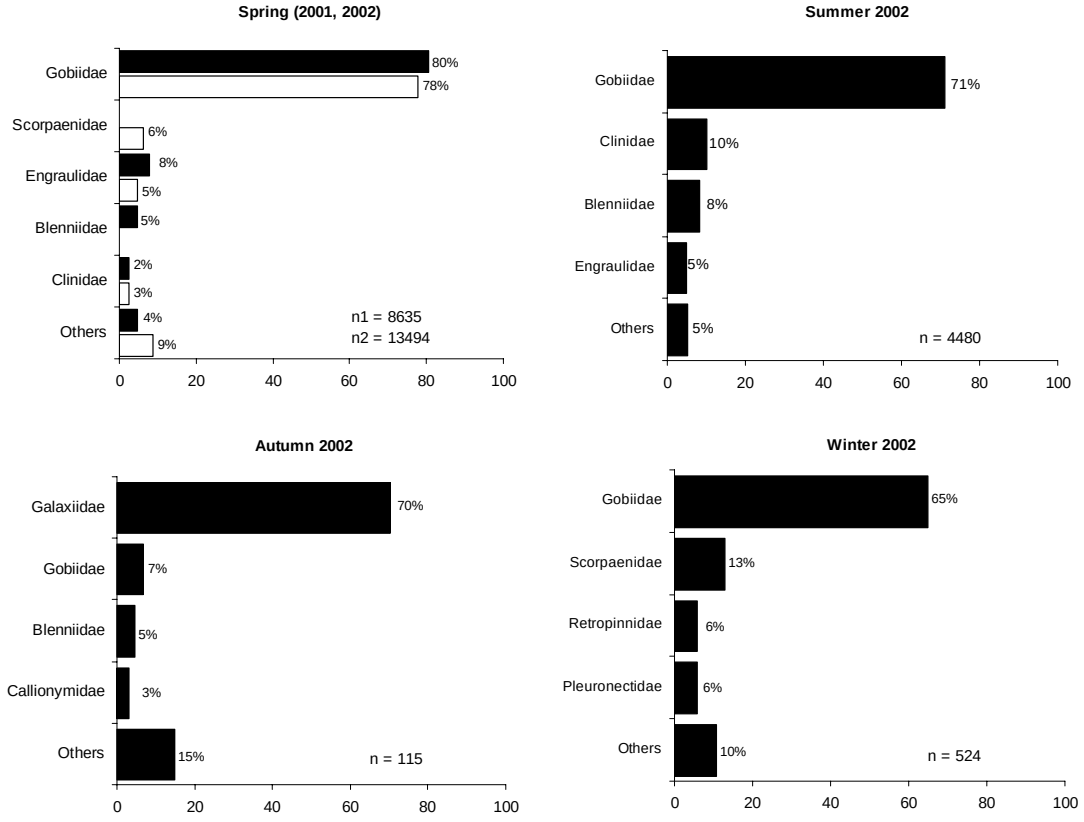

Figure 4.2. Percentage contribution (%) of the most abundant families to the larval fish assemblage by season in the Tamar Estuary during this study. Percentages were derived from total abundances standardized to 100 m^3. n1= Spring 2001 (black bars) and n2= Spring 2002 (white bars).

4.4.2 Changes in abundance and spatial distribution

Mean monthly concentrations of all larval fishes combined peaked in November both in 2001 (270 larvae/100 m^3) and November 2002 (381 larvae/100 m^3), and were lowest in June 2002 (0.3 larvae/100 m^3). Mean water temperatures during highest and lowest larval concentrations were ~15.5˚C and 11˚C, respectively (Fig. 4.1a,c, details on the statistics in Appendix A7-9). Mean larval fish concentrations followed a similar temporal pattern to that of mean zooplankton biomass, which showed peaks in

November both in 2001 (4.1 g/100 m^3) and 2002 (1.1 g/100 m^3), and a low in July 2002 (0.07 g/100 m^3) (Fig. 4.1b).

Larval fish concentrations followed a similar temporal pattern in all salinity regions, with larval concentrations peaking mostly in November both in 2001 and 2002 in all regions (Figs 4.3, 4.4). No significant differences were found in the larval fish concentrations by Venice salinity regions during high concentration periods (October - December 2001 and October and November 2002), except in October 2002, when concentrations were slightly higher in the euhaline and polyhaline region (Table 4.3).

Table 4.3. Results of one-way ANOVAs (ln-transformed data) of larval fish concentrations by Venice salinity regions for months of peak concentrations. Tukey tests were performed when the spatial difference was significant. Abbreviations: E, euhaline; P, polyhaline; M, mesohaline; NS, not significant; ***P*<0.01.

	SS	df	MS	F	*P*	Tukey test
Oct 2001	5.06	2.00	2.53	3.27	NS	
Nov 2001	4.81	2.00	2.40	3.61	NS	
Dec 2001	2.73	2.00	1.36	2.98	NS	
Oct 2002	23.50	2.00	11.75	9.84	**	E P M
Nov 2002	0.90	1.00	0.90	0.99	NS	

Temperature, zooplankton biomass and freshwater flow explained 72% of the variability in larval fish concentrations (*P*<0.001), with temperature being the most significant. By contrast, rainfall and salinity were not significant (Table 4.4).

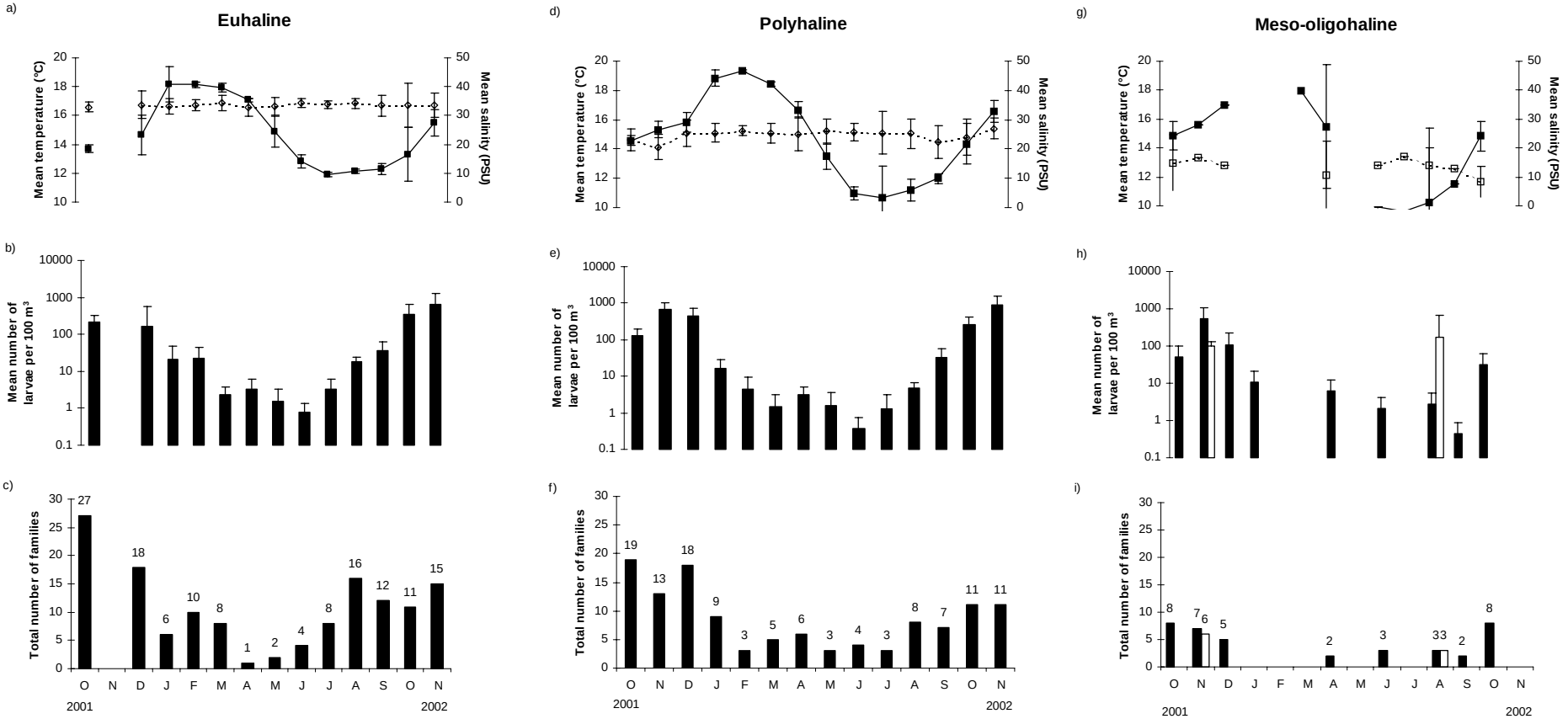

Figure 4.3. Mean monthly (± 95% C.I.) in temperature (°C, —) and salinity (PSU, ---), concentrations of larval fishes (larvae/100 m^3, log-scale) and total number of families in the euhaline (a-c), polyhaline (d-f), mesohaline (black bars) and oligohaline (white bars) (g-i) regions between October 2001 and November 2002. Values above bars in c, f and i correspond to total number of families.

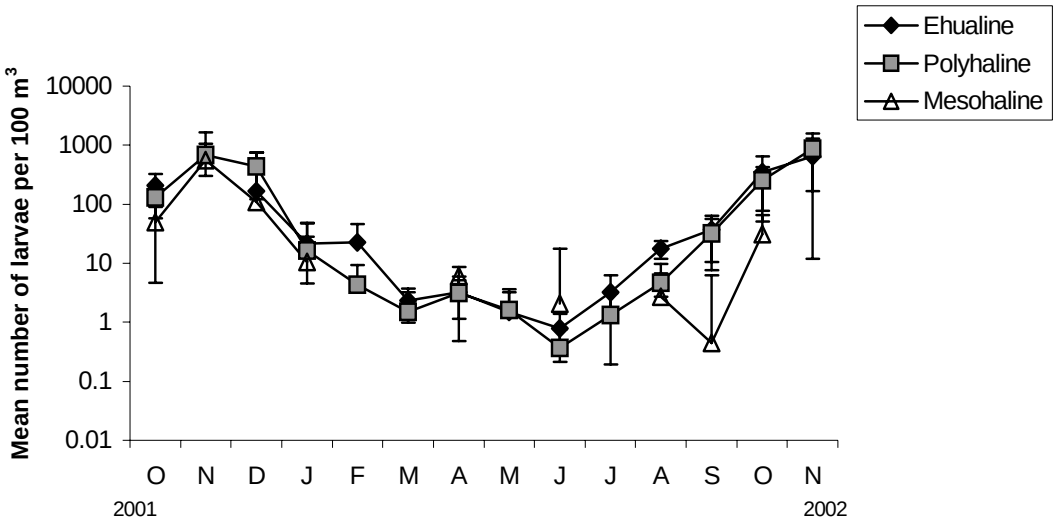

Figure 4.4. Comparison of mean (±95% C.I.) monthly larval fish concentrations (log-scale) between the euhaline, polyhaline and mesohaline regions in the Tamar Estuary during the study period.

Table 4.4. Stepwise multiple linear regression analyses of larval fish concentrations versus zooplankton biomass and environmental factors (temperature, freshwater flow, rainfall and salinity). Abbreviations: adjR^2 = adjusted correlation coefficient, F = F statistics, Beta = individual standardized regression coefficient, B = raw relation coefficients. NS, not significant; *P<0.05; ***P<0.001.

R=0.86	adjR^2=0.72	F=33.94	***
	Beta	B	*P*
Temperature	0.41	4.12	***
Zooplankton biomass	0.19	0.26	*
Freshwater flow	-0.16	-0.71	*
Rainfall	0.14	0.29	NS
Salinity	-0.18	-0.64	NS

4.4.3 Temporal and spatial distribution of abundant families

Gobiidae

Gobiid larvae occurred in all months of the study, with concentrations peaking in November both in 2001 (481 larvae/100 m^3) and 2002 (598 larvae/100 m^3) and was

lowest (<0.1 larvae/100 m^3) in May 2002 (Fig. 4.5a, details in Appendix A-10). Mean concentrations of gobiid larvae did not differ by Venice salinity regions and were caught in all salinities (Figs 4.6a, 4.7). Zooplankton biomass explained 25% of the variability in gobiid concentrations (P<0.001) (Table 4.6).

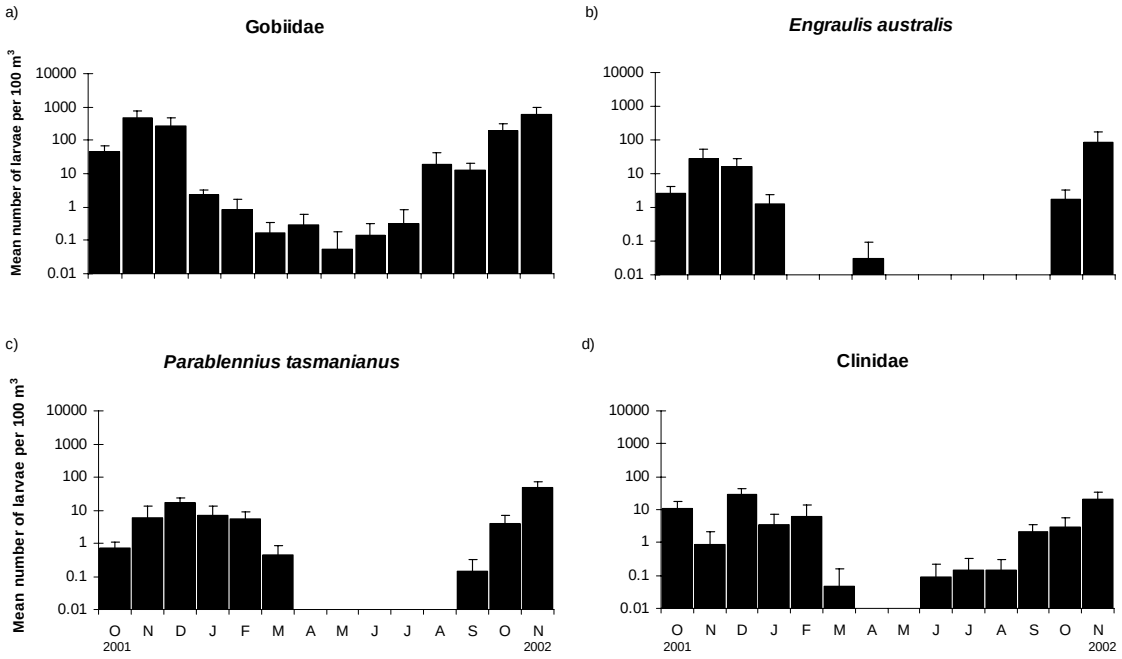

Figure 4.5. Mean monthly (+95% C.I.) larval concentrations (log-scale) of a) Gobiidae, b) *Engraulis australis*, c) *Parablennius tasmanianus* and d) Clinidae in the Tamar Estuary between October 2001 and November 2002.

Engraulidae

Larvae of anchovy *Engraulis australis* occurred only during October 2001 - January 2002, April 2002, and October - November 2002 (Fig. 4.5b). Concentrations peaked in November both in 2001 (28.5 larvae/100 m^3) and 2002 (85.3 larvae/100 m^3) and were lowest in April 2002 (0.03 larvae/100 m^3). Mean concentrations differed significantly by Venice salinity regions (P<0.001) during October 2001 and October and November 2002, with higher concentrations recorded mostly in the polyhaline

region (Table 4.5; Fig. 4.6b). Anchovy larvae occurred in high concentrations between 30 and 40 km upstream from the estuary mouth, at temperatures of ~16-17°C and salinities of ~15-25 PSU (Fig. 4.7). Zooplankton biomass and Venice salinity region (P<0.001) explained 22% of the variability in anchovy concentrations (Table 4.6).

Table 4.5. Results from one-way ANOVAs and Tukey test for mean larval concentrations of *Engraulis australis*, *Parablennius tasmanianus* and Clinidae by salinity region during peak concentration period (October - December 2001 and October and November 2002). Abbreviations: E, euhaline; P, polyhaline; M, mesohaline, NS, not significant; *P<0.05; **P<0.01; ***P<0.001.

	SS	df	MS	F	*P*	Tukey test
E. australis						
October 2001	6.12	2.00	3.06	17.89	***	E M P
November 2001	1.15	1.00	1.15	1.47	NS	
December 2001	1.21	2.00	0.60	3.51	NS	
October 2002	5.39	2.00	2.69	26.71	***	E M P
November 2002	16.53	1.00	16.53	20.00	**	E P
P. tasmanianus						
October 2001	2.02	2.00	1.01	5.43	*	E P M
November 2001	5.03	1.00	5.03	13.57	**	P M
December 2001	1.15	2.00	0.57	10.79	**	E P M
October 2002	6.79	2.00	3.39	25.00	***	E P M
November 2002	0.12	1.00	0.12	0.25	NS	
Clinidae						
October 2001	27.57	2.00	13.79	29.42	***	E P M
November 2001	1.54	1.00	1.54	4.49	NS	
December 2001	19.32	2.00	9.66	14.69	**	E P M
October 2002	12.04	2.00	6.02	20.39	***	E P M
November 2002	10.10	1.00	10.10	9.04	*	E P

Blenniidae

Blenniid larvae, *Parablennius tasmanianus*, were caught only from October 2001 to March 2002, and from September to November 2002 (Fig. 4.5c). Concentrations

peaked during December 2001 (17 larvae/100 m^3) and November 2002 (47 larvae/100 m^3), and were lowest in September 2002 (0.1 larvae/100 m^3). Mean concentrations differed significantly by Venice salinity regions during the peak concentration period (P<0.001), with the lowest concentrations recorded in the mesohaline region (Table 4.5; Fig. 4.6c). Larval blenniids were caught in high concentrations between ~10 and 20 km upstream from the estuary mouth, at temperatures of ~16°C and salinities of ~25-35 PSU (Fig. 4.7). Temperature, freshwater flow and zooplankton biomass explained almost 20% of variability in larval blenniid concentrations (P<0.05) (Table 4.6).

Table 4.6. Stepwise multiple linear regression analyses of larval concentrations of the most abundant taxa by zooplankton biomass and environmental factors. Only significant variables are shown. adjR^2 = adjusted correlation coefficient, F = F statistics, Beta = individual standardized regression coefficient, B = raw relation coefficients. *P<0.05; ***P<0.001.

Overall model results					Regression coefficients of individual variables			
	R	adjR2	F	*P*	Variable	Beta	B	*P*
Gobiidae								
	0.51	0.25	32.7	***	Zooplankton biomass	0.5	2.6	***
E. australis								
	0.51	0.22	6.3	***	Biomass	0.4	1.1	***
					Venice region	0.3	0.5	*
P. tasmanianus								
	0.48	0.2	6.9	***	Temperature	0.2	1.6	*
					Freshwater flow	-0.2	-0.7	*
					Zooplankton biomass	0.2	0.7	*
Clinidae								
	0.41	0.16	9.8	***	Venice region	-0.4	-0.7	***

Clinidae

Clinid larvae occurred in all months except April and May 2002, with high concentrations recorded in December 2001 (28 larvae/100 m^3) and November 2002

(21 larvae/100 m^3), and the lowest in March 2002 (<0.1 larvae/100 m^3) (Fig. 4.5d). Mean concentrations differed significantly by Venice salinity regions during the peak concentration period (P<0.001), with the highest concentrations recorded in the euhaline region, and no larvae caught in the mesohaline region (Table 4.5; Fig. 4.6d). Larval clinids were caught in high concentrations between the entrance channel and 20 km upstream from the estuary mouth, at temperatures of ~13-16°C and salinities of ~25-35 PSU (Fig. 4.7). Venice salinity region explained 16% of variability in larval clinid concentrations (P<0.001) (Table 4.6).

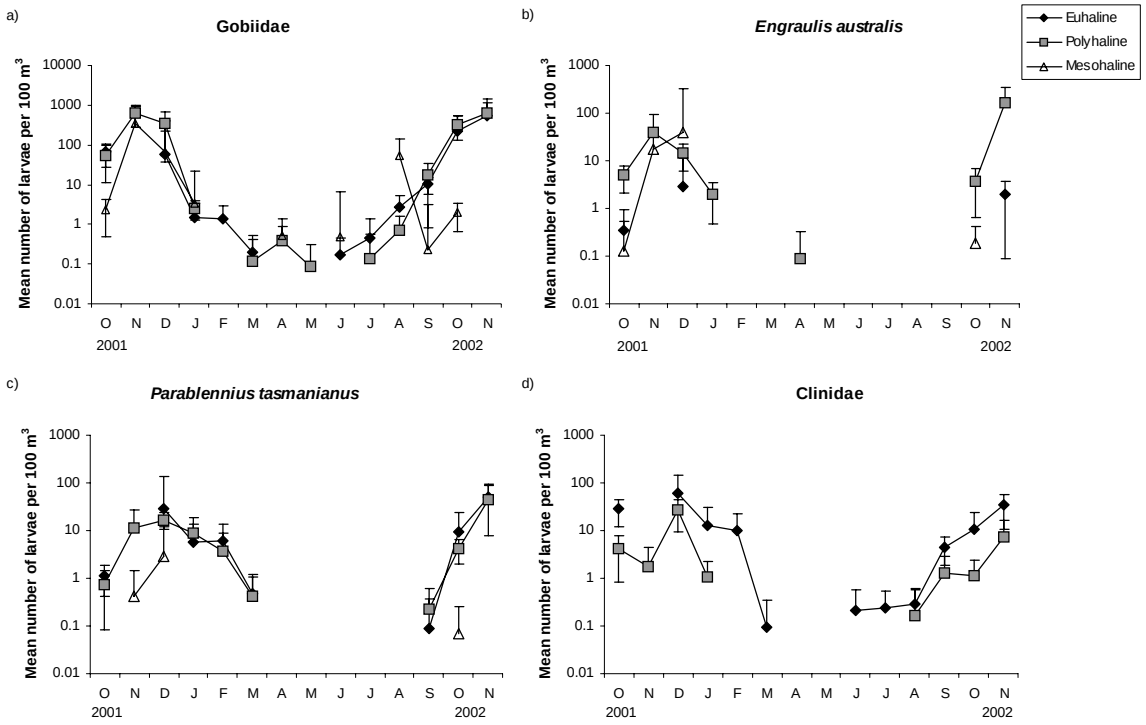

Figure 4.6. Mean monthly (+95% C.I.) larval concentrations (log-scale) of a) Gobiidae, b) *Engraulis australis*, c) *Parablennius tasmanianus*, and d) Clinidae in the euhaline, polyhaline and mesohaline regions in the Tamar Estuary between October 2001 and November 2002.

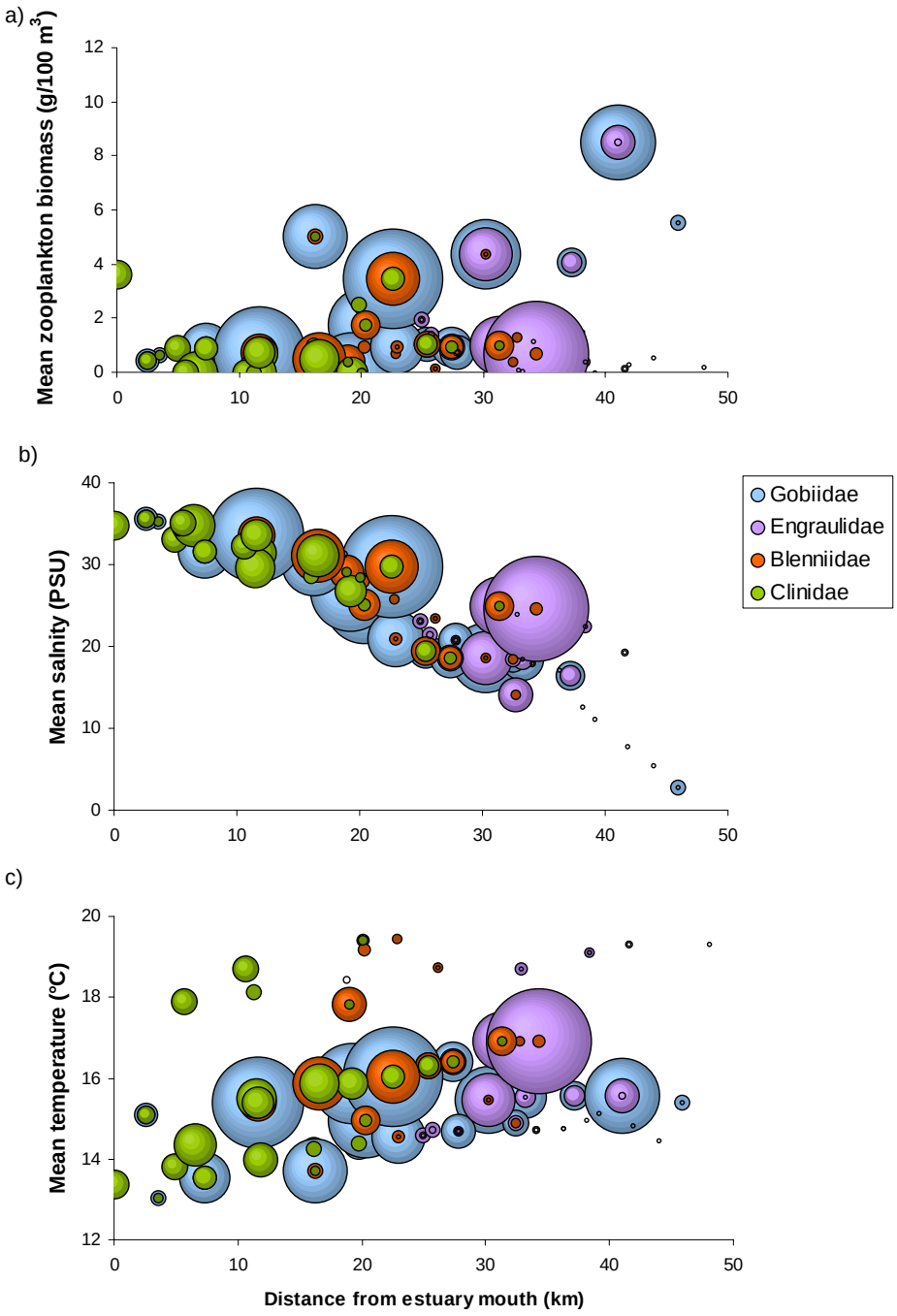

Figure 4.7. Bubble plots showing spatial distribution of larvae of the four most abundant families along the Tamar Estuary (larvae/100 m^3) in relation to a) zooplankton biomass, b) salinity and c) temperature during the peak concentration period (October 2001 - February 2002 and October - November 2002). Size of bubbles is proportional to mean larval concentrations.

4.4.4 Classification and ordination

Classification of sites sampled during the peak concentration period using mean concentrations of larvae from 25 families clearly distinguished two different groups (P<0.001) (Fig. 4.8a).

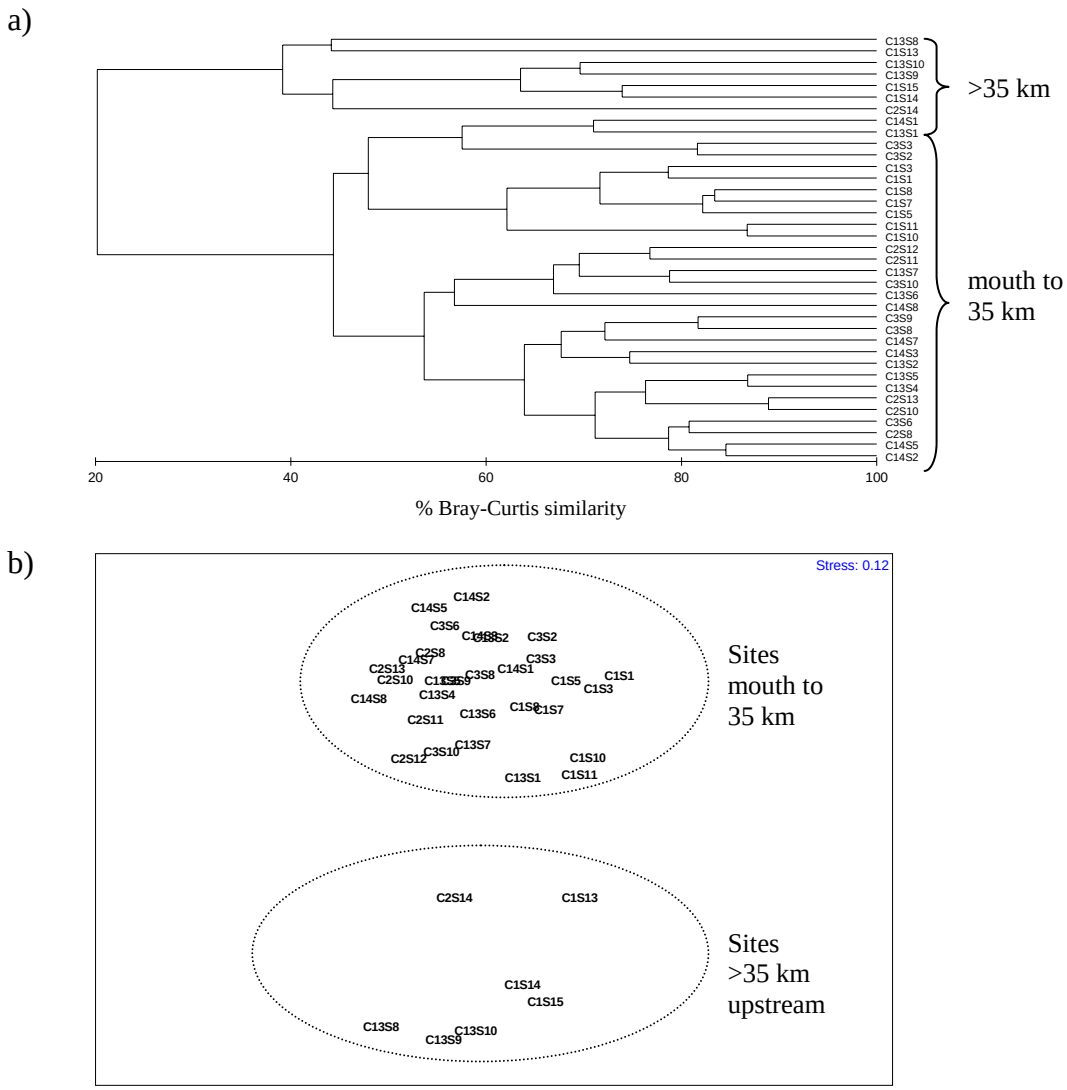

Figure 4.8. a) Group average classification and b) non-parametric multidimensional scaling ordination of sites sampled along the Tamar Estuary during the peak concentration period (October - December 2001 and October and November 2002), based on mean concentrations of larval fishes of 25 families. The % similarity of the classification corresponds to the Bray-Curtis similarity.

The first group comprised sites located within the first 35 km from the estuary mouth clustered at >40% similarity, and were mostly represented by marine/estuarine-spawned larvae belonging to gobiids, anchovy, blenniids, clinids and scorpaenids. The second group comprised sites located >35 km upstream, and were represented mainly by larval galaxiids. Non-parametric multiple dimensional scaling (NMDS) ordination supported the classification by separating sites located >35 km upstream from other sites (Fig 4.8b). The distribution of the two assemblages along the estuary during that period was related to salinity by a $\rho = 0.54$ (BIO-ENV).

4.5 Discussion

This study constitutes the first descriptive account of larval fishes of an estuary anywhere in Tasmania. In the absence of comparable data from other Tasmanian estuaries, results of this intensive study indicate that the larval fish assemblage of the Tamar Estuary shares many characteristics typical of those found in estuaries and enclosed bays in temperate mainland Australia and elsewhere (Beckley, 1985; Roper, 1986; Potter *et al.*, 1990; Neira *et al.*, 1992; Neira and Potter, 1992a; Newton, 1996; Keller *et al.*, 1999; Sutherland and Closs, 2001; Strydom *et al.*, 2003). As with those systems, the assemblage in the Tamar Estuary was dominated by larvae such as gobiids, anchovy, clinids and blenniids, with gobiids being the dominant family.

The total number of families represented by larvae in the Tamar Estuary (38) was also similar and sometimes higher than that reported for other temperate estuaries and enclosed bays in Australia and overseas, including Swan Estuary (37), Wilson Inlet (39), Hopkins River (9), Lake Macquarie (41) and Blackwood Estuary (37) in

Australia; Whangateau Harbour Estuary (23) and Taieri/Waipori River Estuary (7) in New Zealand; Swartkops Estuary (23), Kromme Estuary (12) and Gamtoos Estuary (15) in South Africa; Cadiz Bay (21) in Spain and Middle Atlantic Bight Estuary (43) and Narragansett Bay (25) in the United States (Beckley, 1985; Roper, 1986; Potter *et al.*, 1990; Drake and Arias, 1991; Neira *et al.*, 1992; Neira and Potter, 1992a; Newton, 1996; Keller *et al.*, 1999; Witting *et al.*, 1999; Sutherland and Closs, 2001; Trnski, 2001; Neira and Sporcic, 2002; Strydom *et al.*, 2003). In addition, the number of larval families in the Tamar was also higher compared to known records of adult families (24) (Jordan *et al.*, 1998; Edgar *et al.*, 1999). Of all larval families caught in the estuary, eighteen families have not yet been reported as adults in the estuary, including larvae such as Tripterygiidae, Pomacentridae and Centrolophidae. On the other hand, two adult families, namely Arripidae and Enoplosidae, have not been found as larvae within the system. This difference between the number of larval and adult fish families could be due to a smaller surveyed area and lower sampling intensity from the previous studies. In addition, most of the 38 larval families were caught in the euhaline region, i.e. lower estuary, suggesting that most of the larval families recorded in this study are marine-spawned larvae and marine stragglers, typical of estuary entrances (Beckley, 1986; Roper, 1986; Steffe and Pease, 1988; Drake and Arias, 1991; Neira *et al.*, 1992; Neira and Potter, 1994; Keller *et al.*, 1999)

The peaks in larval fish concentration in the Tamar Estuary (October - December 2001 and October and November 2002) are clearly dominated by the spawning timing of the most abundant families such as gobiids, clinids, blenniids and the anchovy *E. australis*. The timing of those peaks in larval fish concentrations, which occurred ~3 months before the highest temperatures, paralleled that observed in other temperate

bays and estuaries in the Southern Hemisphere, including Algoa Bay, Whangateau Harbour, Swan Estuary and Botany Bay (Beckley, 1986; Roper, 1986; Steffe and Pease, 1988; Neira *et al.*, 1992). The temporal trend followed by the larval fish concentrations was similar to that of zooplankton biomass, both of which were closely related to the temperature cycle in the estuary. A plausible explanation of the close association between temperature, zooplankton biomass and larval fish concentrations is that the spawning timing of temperate fish species does coincide with favourable conditions of temperature and food availability for larvae to survive (Bye, 1984).

The lack of an evident spatial pattern in larval fish concentrations with Venice salinity regions differed from that reported in temperate estuaries in South Africa, where higher larval concentrations were typical in the mesohaline region (Strydom, 2002). This absence of a spatial pattern was also evident in the case of overall zooplankton biomass which showed no association with Venice region. A likely explanation for the lack of spatial structuring by salinity regions is that high current velocities (~2 m/s) may be redistributing concentrations more uniformly along the estuary. It is also possible, however, that the lack of enough data of larval concentrations from the mesohaline and oligohaline regions was the cause of such an absence.

The overall spatial and temporal dominance of larval gobiids in the assemblage in the Tamar Estuary is typical of many temperate estuaries worldwide (Potts, 1984). Gobiids are one of the most successful fish groups in estuaries, adapted to survive such harsh environments through various adaptations, including repeat spawning of demersal eggs over a protracted period of time (Miller, 1984). These adaptations enable gobiids to secure the recruitment of larvae in environments where larval loss

could be high, like in the case of the Tamar Estuary where strong tidal currents produce a net seaward flow at all depths. The fact that the seasonality of larval gobiids followed a similar trend to that of zooplankton biomass illustrates that the spawning period of gobiids in the Tamar Estuary may be strongly linked to food availability, while their spawning frequency may be influenced mostly by changes in temperature (Miller, 1984).

The presence of larvae of anchovy (*E. australis*) in the Tamar Estuary during this study was not surprising, as this temperate species is known to spawn in estuaries and enclosed bays in Australia as well as coastal waters. In addition, their distribution along the middle and upper reaches of the Tamar Estuary (poly and mesohaline regions) parallels that in other temperate estuaries in Australia, and could reflect the distribution of the adult population in these estuary regions (Arnott and McKinnon, 1985; Neira *et al.*, 1992; Neira and Potter, 1992a,b, 1994; Newton, 1996; Neira and Sporcic, 2002). It is also likely that the upstream spawning of anchovy in the Tamar Estuary could help reduce larval loss from this highly flushed system (Newton, 1996), which will enable larvae to take advantage of the high food supply that the estuary provides. However, studies carried out in the coastal area around the mouth of the Tamar Estuary and within the entrance suggest that anchovy also spawn in coastal waters (Raudzens, 2002, 2006). On the other hand, most anchovy larvae collected in those studies were postflexion, with very small amount of preflexion larvae. This suggests that although anchovy spawn in coastal areas, most larvae may have been spawned within the estuary, given the large amount of eggs collected ~35 km upstream, and the fact that most larvae were early preflexion stage.

Unlike anchovy larvae, clinid and blenniid larvae were caught predominantly in the euhaline and polyhaline regions. The presence of high concentrations of larval blenniids between 10 and 20 km upstream from the estuary mouth indicates that these larvae were spawned within the estuary, which parallels the situation with members of this family in other estuaries in temperate Australia and South Africa (Whitfield, 1989; Gaughan *et al.*, 1990; Neira *et al.*, 1992; Newton, 1996; Strydom *et al.*, 2003). Larval clinids, on the other hand, appeared to be less tolerant to lower salinities, as indicated by their higher concentrations in the euhaline region that decreased rapidly upstream. The distribution of larvae of this family is likely to reflect the marine distribution of adult clinid species around and within the entrance of the Tamar Estuary, as supported Raudzens (2002, 2006), who reported larval clinids in the nearshore area around the estuary mouth and within it. This distribution pattern has also been reported in estuaries in South Africa, where clinids were found mainly in the euhaline region (Strydom *et al.*, 2003). The fact that larval clinids were caught during most months with no clear temporal peak, suggests that the family may include several species that spawn at different times of the year (Gunn and Thresher, 1991).

Classification and NMDS ordination of sites during the peak spawning period distinguished two main assemblages, one characterized mainly by marine/estuarine-spawned larvae, such as gobiids, anchovy, clinids and blenniids, and the other characterized by freshwater families such as galaxiids. The fact that there was no evident spatial pattern with the Venice salinity regions is probably due to the dominant families being distributed over more than one region. In addition, no clear separation of sites was observed close to the mouth, where the greater number of families were recorded. This contrasts to the situation reported in other estuaries in

temperate Australia and South Africa, where assemblages from sites near the mouth of the estuary are clearly distinct from those well inside the estuary (Neira *et al.*, 1992; Neira and Potter, 1994; Strydom *et al.*, 2003). Although it is clear that salinity was an important factor in defining the spatial distribution and composition of assemblages in the Tamar, the strong dominance of estuarine-spawned larvae such as most gobiids, blenniids and engraulids, may have masked the contribution of marine-spawned larvae and marine stragglers in the estuary's mouth, which would have in turn resulted in the absence of a distinct assemblage representing the lower estuary. Since salinity limits the distribution of less tolerant species, and freshwater flow changes the chemistry in the water by diluting salinity (Whitfield, 1999), it is not surprising that these factors may be responsible for structuring the larval fish assemblage of the Tamar Estuary into two main groups at the time of peak concentrations.

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Chapter 5

Tidal exchange of larval fishes through the entrance of the Tamar Estuary

5.1 Abstract

The tidal exchange of larval fishes in the entrance of the highly-flushed Tamar Estuary was examined from samples collected during three 24-hour sessions carried out between December 2001 and February 2002. A total of 30,973 larval fishes representing 35 families were collected during the sessions. The most dominant family was the Gobiidae (58.4%), followed by Blenniidae (17.3%), Clinidae (12.8%), Gobiesocidae (3.4%) and Engraulidae (2.1%). Diel phase influenced both the concentrations of most families and community structure significantly more than the tidal phase. While larval fishes from 23 of the 35 families were more abundant at night, only 13 of these displayed tidal behaviour, with four caught exclusively during night ebb: Gerreidae, Ophidiidae, Myctophidae and Serranidae. Of the abundant taxa, blenniid larvae were more abundant during ebb tides regardless of time of day, gobiid and anchovy larvae were most abundant at night on ebb tides, while clinid larvae did not display any evident tidal or diel behaviour. The strong tidal currents in the Tamar Estuary (2 m/s), coupled with the lack of two layered circulation constitute the most likely factors determining the weak tidal pattern in larval concentrations. In the absence of a net upstream bottom flow, the advantage of migrating to a deeper layer during the ebb tides for upstream transport and avoid advection out the system disappears. In addition, the estuary's unique hydrodynamic features may be influencing the distribution of the larval fishes by favouring species with the

appropriate adaptations for highly-flushed environments, i.e. gobiids, while other estuarine-dependent species may enter the estuary at a later stage of development or along the banks to avoid the strong currents.

5.2 Introduction

The role of estuaries in the early life cycles of fishes is of such importance that many of these species have been regarded as estuarine-dependent. Of these, two distinct groups can be recognized, namely (a) those that spawn inside and/or live permanently within estuaries (estuarine residents), and (b) those that spawn outside estuaries and enter these systems as larvae and/or juveniles (marine-estuarine opportunists) (McHugh, 1967; Wallace *et al.*, 1984; Day *et al.*, 1985; Claridge *et al.*, 1986; Lenanton and Potter, 1987; Potter *et al.*, 1990; Keller *et al.*, 1999). For these groups, both transport and retention of early stage fishes within estuaries are of critical importance for the survival and successful recruitment of estuarine-dependent species.

Since most estuaries have a net seaward flow, and early larvae do not posses the swimming ability to overcome these currents (Roper, 1986; Forward Jr *et al.*, 1999), their transport and retention within these systems represent a challenge. It is widely accepted that a combination of passive and active transport is used by larval fishes to enter and remain inside estuaries (Beckley, 1985; Epifanio, 1988; Whitfield, 1989a; Neira *et al.*, 1992; Kingsford and Suthers, 1996; Forward Jr *et al.*, 1999; Trnski, 2001; Hare *et al.*, 2005). Passive transport refers to larval transport controlled exclusively by physical factors, whereas active transport involves changes in larval swimming

behaviour to maintain their horizontal position (Norcross and Shaw, 1984). However, the mechanisms used by larvae to enter and remain within estuaries is species-specific, and may also depend on the developmental stage of larvae, which may involve more active behaviour as larvae mature. Behavioural mechanisms used by larvae to remain in estuaries include selective tidal transport (Weinstein *et al.*, 1980; Fortier and Leggett, 1983; Norcross and Shaw, 1984; Miskiewicz, 1986; Boehlert and Mundy, 1988; Epifanio, 1988; Shaw *et al.*, 1988; Norcross, 1991; Neira and Potter, 1992a; Tzeng and Wang, 1993; Forward Jr *et al.*, 1999), remaining at a fixed depth (Schultz *et al.*, 2000), horizontal migration (Beckley, 1985; Schultz *et al.*, 2000), rapid settling (Whitfield, 1989a) and the use of slow moving water near the banks (Weinstein *et al.*, 1980; Melville-Smith *et al.*, 1981; Pringle, 1982; Whitfield, 1989a; Schultz *et al.*, 2003). Diel migration has also been observed in larval fishes within estuaries, whereby they migrate to the surface at night and towards the bottom during the day (Lyczkowski-Shultz and Steen, 1991; Churchill *et al.*, 1999; Trnski, 2001).

Transport and retention mechanisms utilized by larvae within estuaries may also vary depending on the hydrographic features of individual systems (Weinstein *et al.*, 1980; Fortier and Leggett, 1982; Grioche *et al.*, 1999; Grioche *et al.*, 2000). The usual model to explain transport and retention of larvae in estuaries is based on a two-layered circulation flow, where the upper layer has a net downstream flow and the bottom layer a net upstream flow, with larvae migrating vertically to move in and out of the estuary, i.e. selective tidal transport (Weinstein *et al.*, 1980; Boicourt, 1982; Fortier and Leggett, 1983; Boehlert and Mundy, 1988; Forward Jr *et al.*, 1999; Trnski, 2001).

The Tamar Estuary is a highly-flushed system characterized by weak vertical stratification and strong tidal mixing, indicating a lack of two-layered circulation. Therefore, in the absence of a two-layered circulation, selective tidal transport to explain transport and retention of larvae within two-layered estuaries may not be suitable. This chapter aims to investigate the effect of tides on larval fishes in the entrance of the Tamar Estuary using intensive continuous 24-hour sampling during times of high larval abundance. The results are then used to identify possible mechanisms that may aid in the transport and retention of larval fishes within this highly-flushed system.

5.3 Materials and methods

5.3.1 Data collection and processing

Three 24-hour larval fish sampling sessions were conducted at three fixed sites (sites 2, 3, 6) in the lower Tamar Estuary in December 2001 (11-12th, 9:04-8:16), January 2002 (24-25th, 13:35-11:42) and February 2002 (11-12th, 11:29-10:02) (Fig. 5.1). Sites were sampled at four different tidal conditions, e.g. flood day/night and ebb day/night to account for tidal and diel cycles. Sampling of each tidal condition was carried in ~6 hour period (equivalent to the duration of a tidal phase).

Vertical profiles of temperature (^{o}C) and salinity (PSU) were obtained at each of the three sites sampled during the 24-hour sessions with a calibrated Seabird Electronics SBE 19 Conductivity-Temperature-Depth (CTD) profiler. Additional environmental data during the sampling period December 2001 – February 2002 were also obtained

at sites 1, 4 and 5 (Fig. 5.1). All six sites were sampled in the same order each time, i.e. site 1 at the start of each tide (low/high tide), and sites 3 and 4 during mid-tide. Environmental data were transformed into text files using the manufacturer's software and cleared of noise. Acoustic backscatter strength (dB) data were recorded continuously during the sampling sessions using a 600 kHz Acoustic Doppler Current Profiler (ADCP; Workhorse Rio Grande, RDI). These data were averaged into 1-minute intervals, with a vertical resolution of 50 bins, each 0.5 m deep, and processed with TRANSECT (RDI, 2000).

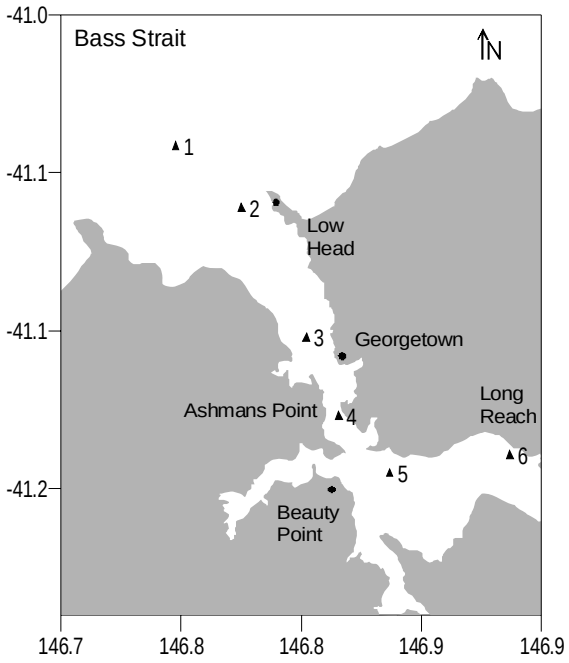

Figure 5.1. Map of the lower Tamar Estuary in northern Tasmania, showing the location of the six sites sampled during the 24-hour sessions carried out monthly between December 2001 and February 2002. Larval fishes were collected at sites 2, 3 and 6, whereas environmental factors were obtained in all sites.

Plankton samples were collected simultaneously at two different depth stratums, i.e. 0-10 and 10-20 m, using two bongo samplers each fitted with two 500 μm mesh nets. A purpose made opening-closing mechanism was fitted to the mouth of each net to

obtain samples at the different depth strata. This mechanism consisted of nylon sheaths inside the mouth of each net that were connected with ropes to enable the sheaths to be closed and open at the desired depth. The samplers were lowered directly from the stern of a 14 m steel hull vessel to 10 and 20 m, and then brought back in a step-wise mode. Tows were conducted for 10 minutes at a speed of ~3 knots, and depth of nets was estimated by measuring the length and angle of the cable. A replicate sample was taken at every site and depth strata. Total water volume filtered during each tow (m^3) was calculated from counts obtained with General Oceanics flowmeters attached to the mouth of each net. Samples were fixed on board in 10% formalin-seawater, and later preserved in 70% ethanol. In all, the study yielded a total of 144 plankton samples from three 24-hour sampling sessions.

All samples were sorted under a dissecting stereomicroscope and all larval fishes removed, counted and identified to family level. Identifications were carried out using the larval fish guides of Neira *et al.* (1998) and Leis & Carson-Ewart (2000), and the adult fish guide of Gomon *et al.* (1994). Larval fishes that could not be identified to any taxonomic level, i.e. damaged larvae and/or small yolk sac individuals, were placed under the "unidentified" category. Visual inspection of the larval fish samples was performed to examine the larval stage of the most dominant families.

5.3.2 Data analyses

Temperature and salinity data from each site were averaged over depth, tide and time, and plotted for each month. Acoustic data from each depth cell was converted into backscatter strength (*Sv*) using the modified sonar equation from Deines (1999) (see Chapter 3 for details).

The total number of larval fishes from the two nets of the bongo sampler were added and standardised to numbers per 100 m^3, before replicates were averaged. Percentage contributions of families and those of selected individual taxa to the total assemblage were calculated using standardized concentrations.

Multiple factorial analyses of variance were performed using STATISTICA® to ascertain whether the larval fish concentrations differed significantly among months and tides. Each month was also analysed separately to test for any spatial, tidal and diel variation. All data were ln-transformed to conform to normality and homogeneity of variance. Preliminary analyses of some of the data showed that there was significant interaction between the factors and due to the complexity of the interactions it was deemed unnecessary to continue with the analyses. Tukey tests were only performed when the effect of the factor was significant but the interaction not significant. Tidal, diel and spatial variability in the concentrations of the four most abundant families was also tested following the same set of analyses.

Non-parametric multivariate analyses were conducted using PRIMER statistical software to asses the temporal variation in the community composition in relation to tidal and diel cycles, as well as month (Clarke, 1993; Warwick, 1993; 1999). Concentration data (larvae/100 m^3) per family, month and tide were square-root transformed, and a Bray-Curtis similarity matrix generated. Classification and multidimensional scaling (NMDS) ordination were performed on this matrix to assess relationships between larval fish assemblages among different months and tides. These analyses were followed by analyses of similarities (ANOSIM) to detect any

significant differences between the groups formed by the classification and NMDS analyses, and a SIMPER routine to determine which key families contributed to the similarities or differences between groups. All 35 families, including those with <0.1% contribution were used for the analyses. The inclusion of all families was to examine if incidental species occurred at a particular tide.

5.4 Results

5.4.1 Environmental factors

Mean salinity during December 2001 decreased from ~35 PSU at site 1 to ~27 PSU at site 6, some 16 km upstream from the estuary mouth.

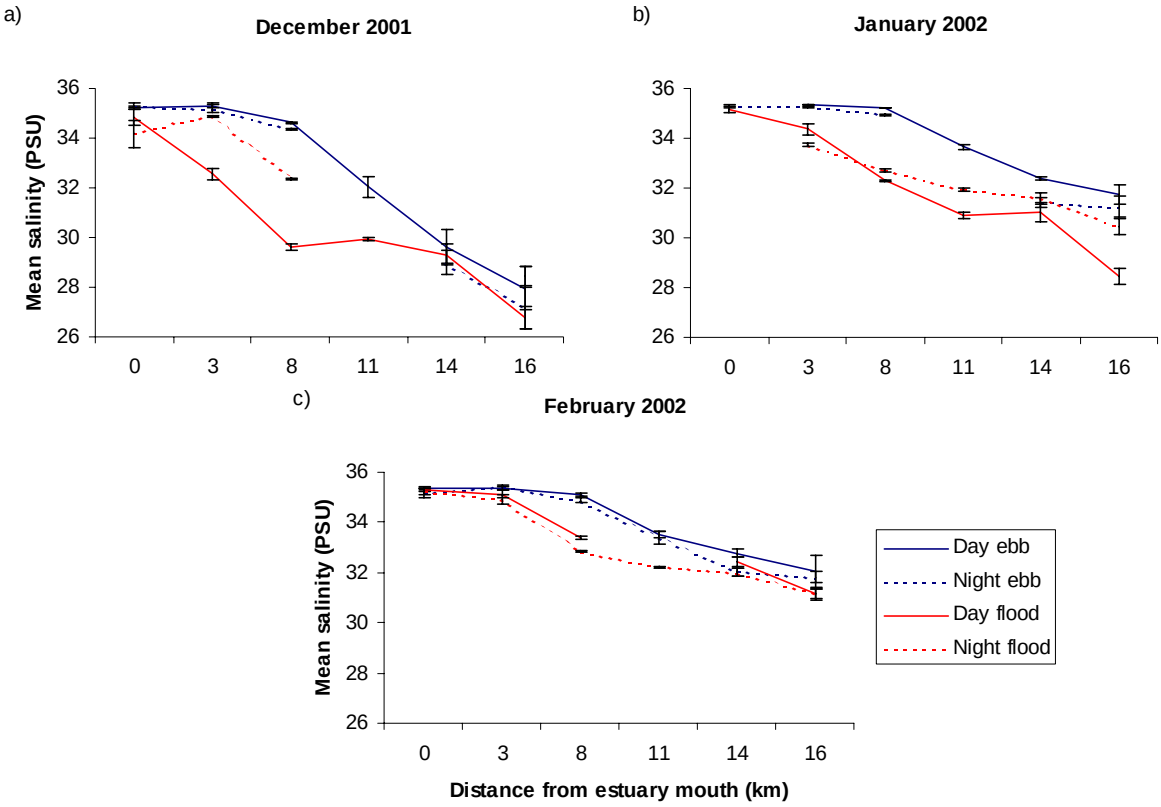

Figure 5.2. Mean monthly (± 95% C.I.) salinities (PSU) along the entrance of the Tamar Estuary during the four tidal conditions sampled between December 2001 and February 2002.

On the other hand, mean salinity only declined to 30-31 PSU at site 6 during January and February 2002 (details in Appendix A11). The greatest salinity difference between ebb and flood tide was recorded at sites between 8 – 14 km, with waters being on average less saline during flood than during ebb tide by ~1 PSU.

Mean temperatures along the lower Tamar Estuary in December 2001 increased from 14°C at site 1 to ~16°C at site 6. By contrast, mean temperatures in January and February 2002 remained at 17-18°C at all sites (Fig. 5.3). The greatest temporal variation was observed at site 6, where waters were on average warmer during flood than during ebb tide by ~2°C.

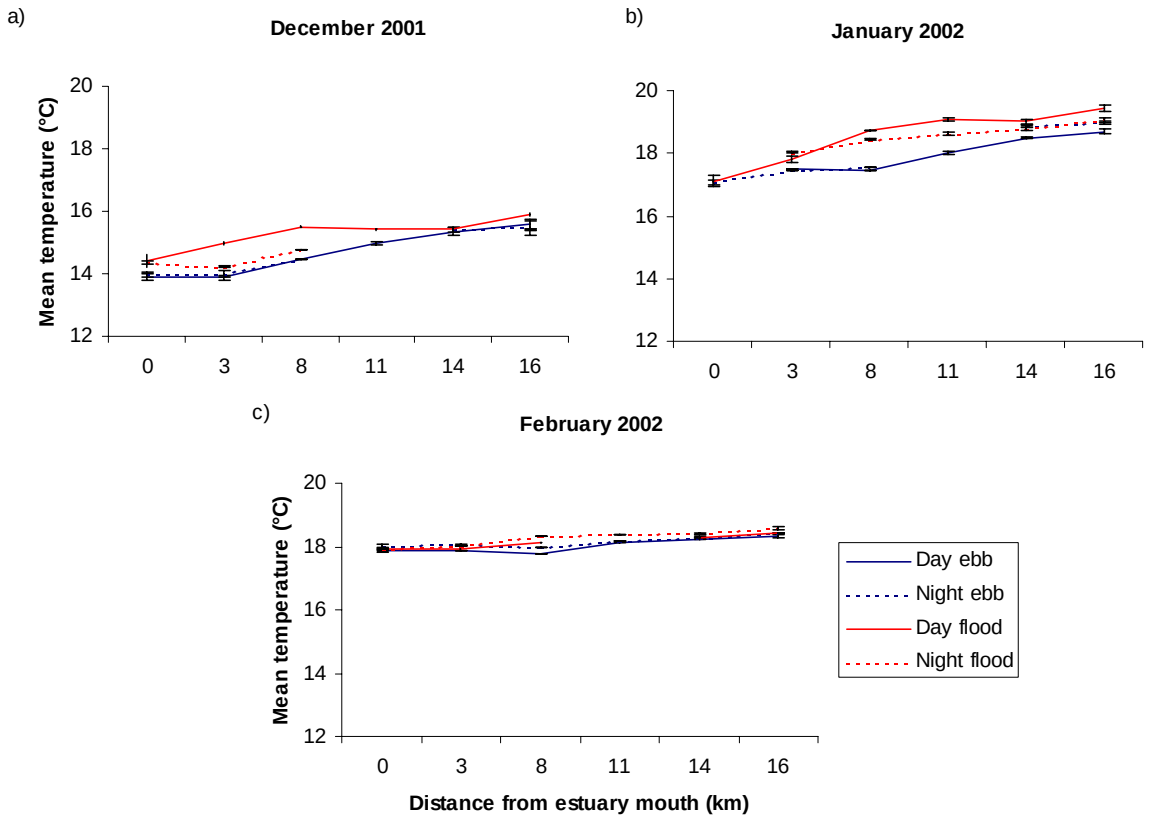

Figure 5.3. Mean monthly (± 95% C.I.) temperatures (°C) along the entrance of the Tamar Estuary during the four tidal conditions sampled between December 2001 and February 2002.

5.4.2 Overall family composition

A total of 30,973 larval fishes representing 35 families were collected during the three 24-hour sampling sessions (Table 5.1). Larval fishes from five families accounted for 94% of the total caught during the experiment (numbers standardised to 100 m^3). Gobiidae was by far the most abundant family, comprising 58.4% of the total number of larvae caught. The Gobiidae was followed by Blenniidae (*Parablennius tasmanianus*) (17.3%), Clinidae (12.8%), Gobiesocidae (3.4%) and Engraulidae (*Engraulis australis*) (2.1%), while the remaining families (6%) each contributed ≤0.2% of the total caught. Three families were represented only by one larva, namely Ophidiidae, Myctophidae and Serranidae.

Of the 35 families identified, larvae from seven families (Leptoscopidae, Callionymidae, Gempylidae, Gerreidae, Ophidiidae, Myctophidae and Serranidae) were caught only during ebb tides, four of which were caught exclusively at night, while one family (Clupeidae) was caught during flood tide. Larvae from four families were caught only at night regardless of tide (Sillaginidae, Pempheridae, Apogonidae and Triglidae) and one during the day (Retropinnidae). Larvae from 23 families showed a diel pattern with larvae of 21 families occurring mostly at night time (Table 5.1).

The number of families did not vary greatly among the three months of the study, with the highest number recorded during the night ebb in February 2002 (23) and the lowest during day ebb in the same month (7). The number of families was almost always higher during ebb than during flood tides and during night than during day time (Fig. 5.4).

Table 5.1. Families and taxa of larval fishes caught at the entrance of the Tamar Estuary between December 2001 and February 2002, and their respective ranks, abundance, overall percentage contribution and percentage contribution at each tide. Families for which larvae could not be identified were pooled. Ranks are given when their contribution was ≥0.1%. Ranking and percentage contribution are based on adjusted numbers, which correspond to the sum of the monthly numbers of larvae at each site after they have been standardized to 100 m^3.

N	Family/Taxa	Family Rank	Total contribution	Number caught	Adjusted numbers	Day flood	Day ebb	Night flood	Night ebb	Life cycle category
1	**Gobiidae**	1	58.4	18756	7101.36	78.5	17.1	62.7	64.4	E. O .S
2	**Blenniidae**	2								
	Parablennius tasmanianus		17.3	3644	2100.95	3.7	60.4	6.9	9.0	E
3	**Clinidae**	3	12.8	4478	1553.85	11.0	13.7	16.8	11.4	E, S
4	**Gobiesocidae**	4	3.4	1314	417.27	1.8	1.6	3.0	5.7	S
5	**Engraulidae**	5								
	Engraulis australis		2.1	615	251.98	1.3	1.1	2.7	2.7	E
6	**Monacantidae**	6								
	Brachalutheres jacksonianus		0.2	65	23.14	0.2	0.1	0.3	0.2	S
	Monacanthids		0.9	316	113.76	0.7	0.7	0.9	1.2	S
7	**Tripterygiidae**	7	0.7	324	82.22	0.8	1.5	0.6	0.2	S
8	**Labridae**	8	0.5	286	62.91	0.1	0.9	0.6	0.6	S
9	**Syngnathidae**	9	0.5	166	56.62	0.3	0.2	0.7	0.6	E, S
10	**Tetraodontidae**	10	0.4	72	54.57	0.1	0.3	0.6	0.7	S
12	**Pomacentridae**	11								
	Parma sp.		0.1	51	15.58	<0.1	0.2	<0.1	0.2	S
	Pomacentrids		0.2	48	25.41	0.1	-	0.6	0.2	S
11	**Odacidae**	12	0.3	106	34.94	0.1	0.1	0.5	0.4	S, O
13	**Sillaginidae**	13								
	Sillago flindersi		0.2	83	22.67	-	-	0.1	0.5	S
14	**Pempheridae**	14	0.2	85	20.75	-	-	<0.1	0.4	S
15	**Hemiraphidae**	15	0.1	71	16.90	-	0.3	0.4	<0.1	E
16	**Atherinidae**	16	0.1	49	16.65	0.1	0.1	0.2	0.2	E
17	**Galaxiidae**									
	Galaxias spp.		<0.1	31	6.32	0.1	<0.1	0.1	<0.1	F
18	**Creediidae**		<0.1	22	7.62	<0.1	-	0.1	0.1	E
19	**Platycephalidae**									
	Platycephalus bassensis		<0.1	20	5.69	<0.1	<0.1	0.1	0.1	E
20	**Cynoglossidae**		<0.1	18	4.77	<0.1	-	-	0.1	S
21	**Scorpaenidae**		<0.1	15	3.50	<0.1	<0.1	0.1	<0.1	S
22	**Mullidae**									
	Upeneichthys sp.		<0.1	9	1.94	-	0.1	<0.1	-	S
23	**Gempylidae**									
	Thyrsites atun		<0.1	7	2.66	-	<0.1	-	<0.1	S
24	**Gerreidae**									
	Parequula melbournensis		<0.1	7	1.48	-	-	-	<0.1	S
25	**Apogonidae**		<0.1	5	3.76	-	-	0.1	<0.1	S
26	**Callyonimidae**		<0.1	4	0.91	-	<0.1	-	<0.1	S
27	**Bothidae**		<0.1	4	1.00	<0.1	-	-	<0.1	S

Table 5.1. *Continued*

N	Family/Taxa	Rank	Total contribution	Number caught	Adjusted numbers	Day flood	Day ebb	Night flood	Night ebb	Life cycle category
28	**Retropinnidae**									
	Retropinna sp.		<0.1	4	0.79	<0.1	<0.1	-	-	F
29	**Triglidae**		<0.1	4	1.06	-	-	<0.1	<0.1	S
30	**Pegasidae**		<0.1	3	0.61	<0.1	<0.1	-	<0.1	S
31	**Leptoscopidae**		<0.1	3	2.51	-	0.1	-	<0.1	S
32	**Clupeidae**									
	Spratelloides robustus		<0.1	1	0.34	-	-	<0.1	-	S
	Clupeids		<0.1	1	0.16	<0.1	-	-	-	S
33	**Ophidiidae**		<0.1	1	0.33	-	-	-	<0.1	S
34	**Myctophidae**		<0.1	1	0.32	-	-	-	<0.1	S
35	**Serranidae**		<0.1	1	0.26	-	-	-	<0.1	S
	Unidentified		1.2	283	150.82	0.7	1.4	2.0	1.1	
	Total			**30973**	**12168.36**					

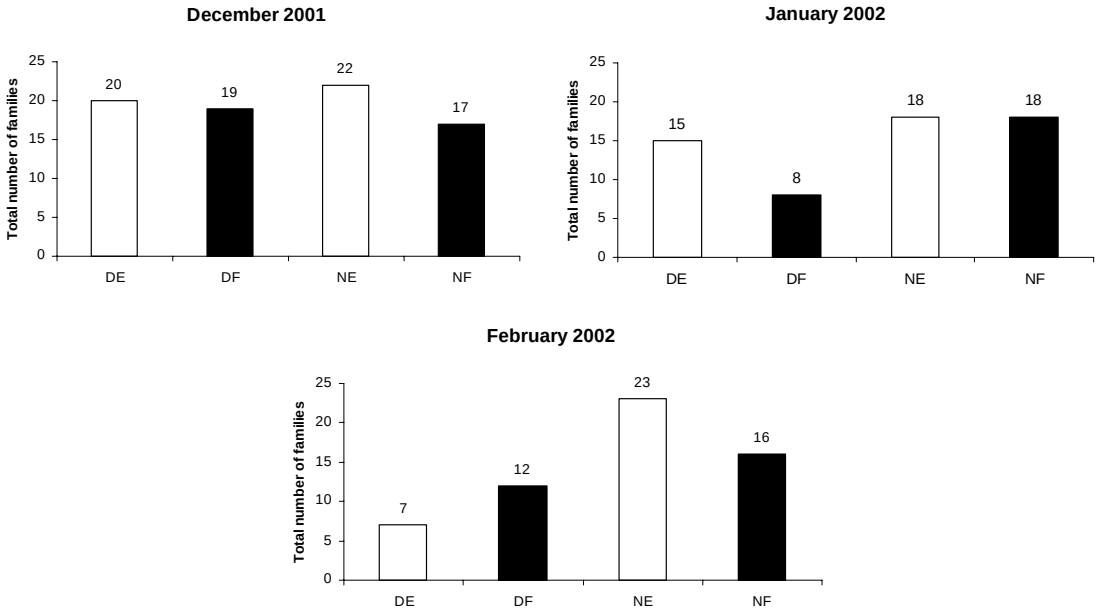

Figure 5.4. Total number of families caught along the entrance of the Tamar Estuary between December 2001 and February 2002 during the four tidal conditions. Numbers above bars indicate number of families. Abbreviations: DE = day ebb; NE = night ebb; DF = day flood; NF = night flood.

5.4.3 Diel and tidal variation in larval fish abundances

The highest larval fish concentrations were recorded during the day flood in December (239 larvae/100 m^3), and the lowest during the night flood in February 2002 (6 larvae/100 m^3) (Fig. 5.5, details in Appendix A11). Monthly mean concentrations of all larval fishes combined varied significantly between months and tides (P<0.001) with a significant interaction (Table 5.2).

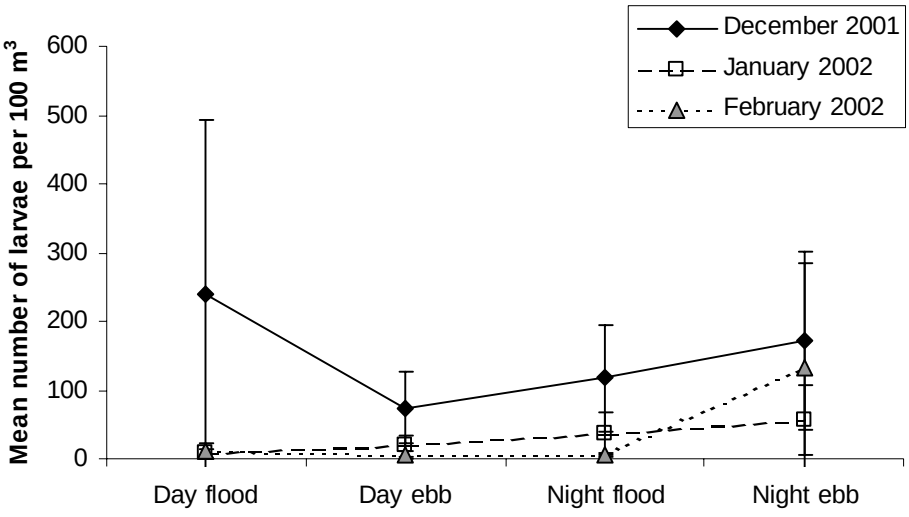

Figure 5.5. Mean (± 95% CI) larval fish concentrations (larvae/100 m^3) obtained at the entrance of the Tamar Estuary between December 2001 and February 2002 during different tidal cycles.

Mean larval fish concentrations during December 2001 varied significantly among tides and sites, but not between depth strata (P< 0.001) (Table 5.3, details in Appendix A12). The greatest (586 larvae/100 m^3) and lowest (16 larvae/100 m^3) larval fish concentrations were recorded at site 6 during day flood and at site 2 during day ebb, respectively (Fig. 5.6). Although there was a significant difference between

tides, no clear diel or tidal pattern in concentrations was observed, with only day ebb differing from the other tides and producing the lowest concentrations.

Table 5.2. Results of multi-factorial ANOVA of mean larval fish concentrations (ln-transformed, larvae/100 m^3) by month and tide/time (ebb day/night, flood day/night). ***P<0.001.

	SS	df	MS	F	P
Month	22.85	2	11.43	105.74	***
Tide/time	10.04	3	3.35	30.98	***
Month x Tide/time	9.60	6	1.60	14.81	***
Error	1.30	12	0.11		

The highest (147 larvae/100 m^3) and lowest (1 larvae/100 m^3) larval fish concentrations during January 2002 were recorded in the 0-10 m stratum at site 3 during night ebb and the 10-20 m stratum at site 6 during day flood, respectively (Fig. 5.6). There was evidence of a diel pattern in the overall larval fish concentrations, with higher concentrations at night than during day time. In addition, larval fish concentrations increased downstream, being higher at sites 2 and 3 and lower at site 6 (Fig. 5.6). Mean larval fish concentrations during January 2002 differed significantly between tide, depth and site, with a significant interaction (P< 0.01) (Table 5.3).

The highest (370 larvae/100 m^3) and lowest (<1 larvae/100 m^3) larval fish concentrations during February 2002 were recorded in the 0-10 m stratum at site 3 during ebb night and the 10-20 m stratum at site 3 during flood day, respectively (Fig. 5.6). There was evidence of diel and tidal patterns in larval fish concentrations, with concentrations being significantly higher during night ebb than during the other tides. Mean larval fish concentrations during February 2002 differed significantly between sites, tides and depth with a significant interaction (P< 0.001) (Table 5.3).

Table 5.3. Results of a three way multi-factorial ANOVA of monthly larval fish concentrations (ln-transformed, larvae/100 m^3) by tide/time (ebb day/night, flood day/night), site (2, 3, 6) and depth (0-10, 10-20). Abbreviations: DF, day flood; NF, night flood; DE, day ebb; NE, night ebb. NS, not significant, **P*<0.05;***P*<0.01, ****P*<0.001.

	SS	df	MS	F	*P*	Tukey test
December 2001						
Tide	7.96	3	2.65	12.29	***	DF NF NE DE
Depth	0.00	1	0.00	0.01	NS	
Site	24.60	2	12.30	56.97	***	2 3 6
Tide x Depth	0.05	3	0.02	0.07	NS	
Site x Tide	2.65	6	0.44	2.05	NS	
Site x Depth	0.01	2	0.01	0.03	NS	
Site x Tide x Depth	0.79	6	0.13	0.61	NS	
Error	5.18	24	0.22			
January 2002						
Tide	22.61	3	7.54	29.40	***	
Depth	2.32	1	2.32	9.03	**	
Site	10.16	2	5.08	19.82	***	
Tide x Depth	0.35	3	0.12	0.46	NS	
Site x Tide	7.71	6	1.29	5.01	**	
Site x Depth	2.78	2	1.39	5.42	*	
Site x Tide x Depth	5.71	6	0.95	3.71	**	
Error	6.15	24	0.26			
February 2002						
Tide	60.73	3	20.24	98.52	***	
Depth	2.12	1	2.12	10.30	**	
Site	4.87	2	2.43	11.85	***	
Tide x Depth	1.04	3	0.35	1.68	NS	
Site x Tide	22.54	6	3.76	18.28	***	
Site x Depth	0.08	2	0.04	0.20	NS	
Site x Tide x Depth	3.33	6	0.56	2.70	*	
Error	4.93	24	0.21			

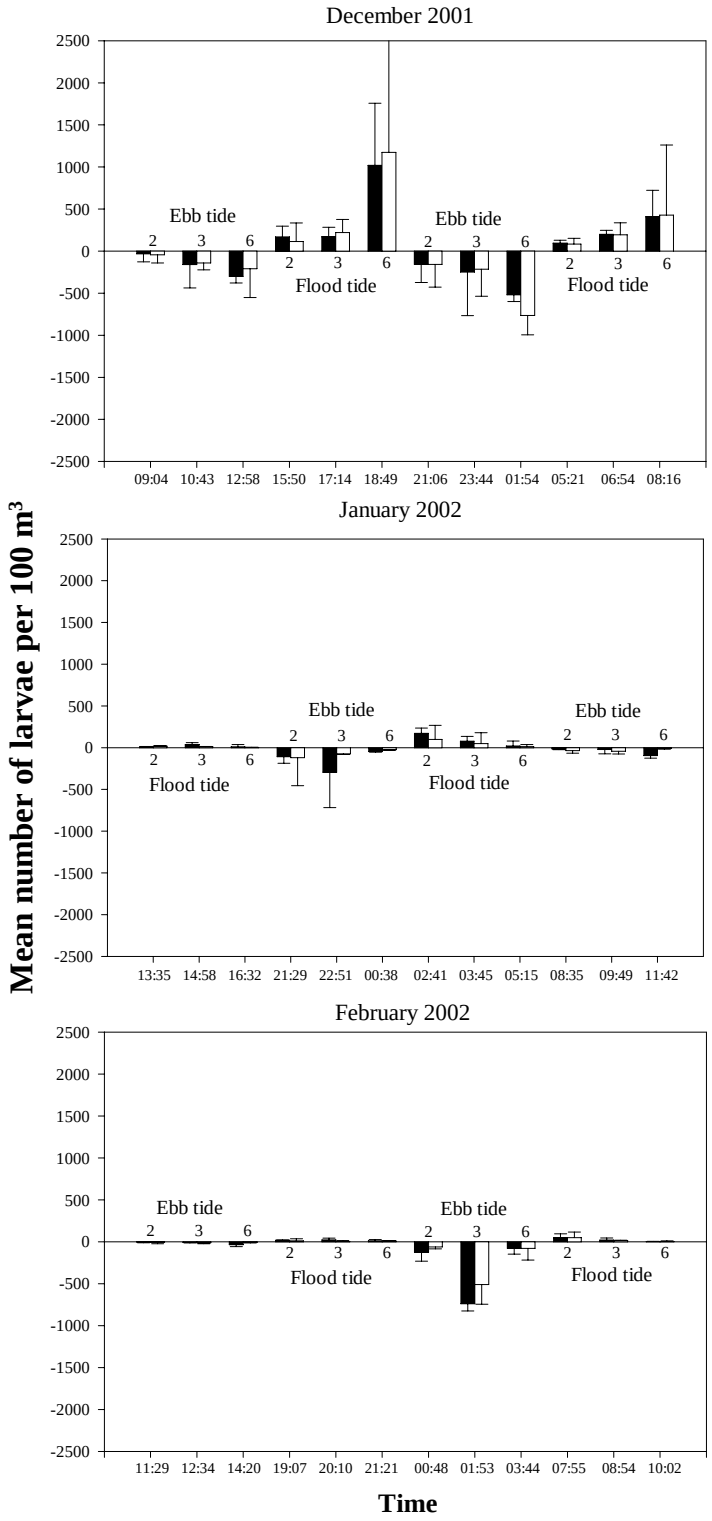

Figure 5.6. Mean (+95 C.I.) larval fish concentrations (larvae/100 m^3) during consecutive tidal cycles along the lower Tamar Estuary between December 2001 and February 2002. Numbers above and below bars indicate the sampling site. Time along the x-axis correspond to Eastern Australian Summer Standard Time. Black bars = 0-10 m depth stratum and white bars = 10-20 m depth stratum.

5.4.4 Larval fish concentration and backscatter strength

Correspondence between larval fish concentrations from nets and acoustic backscatter strength (*Sv*) was observed during December 2001, i.e. high *Sv* spots were recorded at sites where high concentrations of larvae were caught (Fig. 5.7). By contrast, no correspondence between larval fish concentrations and *Sv* was detected in January 2002 during either day flood or ebb (Fig. 5.8). Instead, correspondence improved during night time, when higher *Sv* spots (-68 dB) were recorded together with larval fish concentrations. In addition, very high *Sv* spots (-48 dB) were recorded near the surface both during night ebb and flood, although the sampling sites did not correspond to the location of these spots. A patchier distribution of *Sv* was observed during ebb tides and a more continuous distribution during flood tides. No correspondence between larval fish concentrations and *Sv* was found in any tidal phase during February 2002 (Fig. 5.9). High larval fish concentrations were found during night ebb, but they did not correspond to high *Sv* spots, while very low larval concentrations were obtained in the other tides, regardless of the *Sv* recorded during those times. Overall, *Sv* recorded during February 2002 along the entire transect, was higher at night and during flood tides.

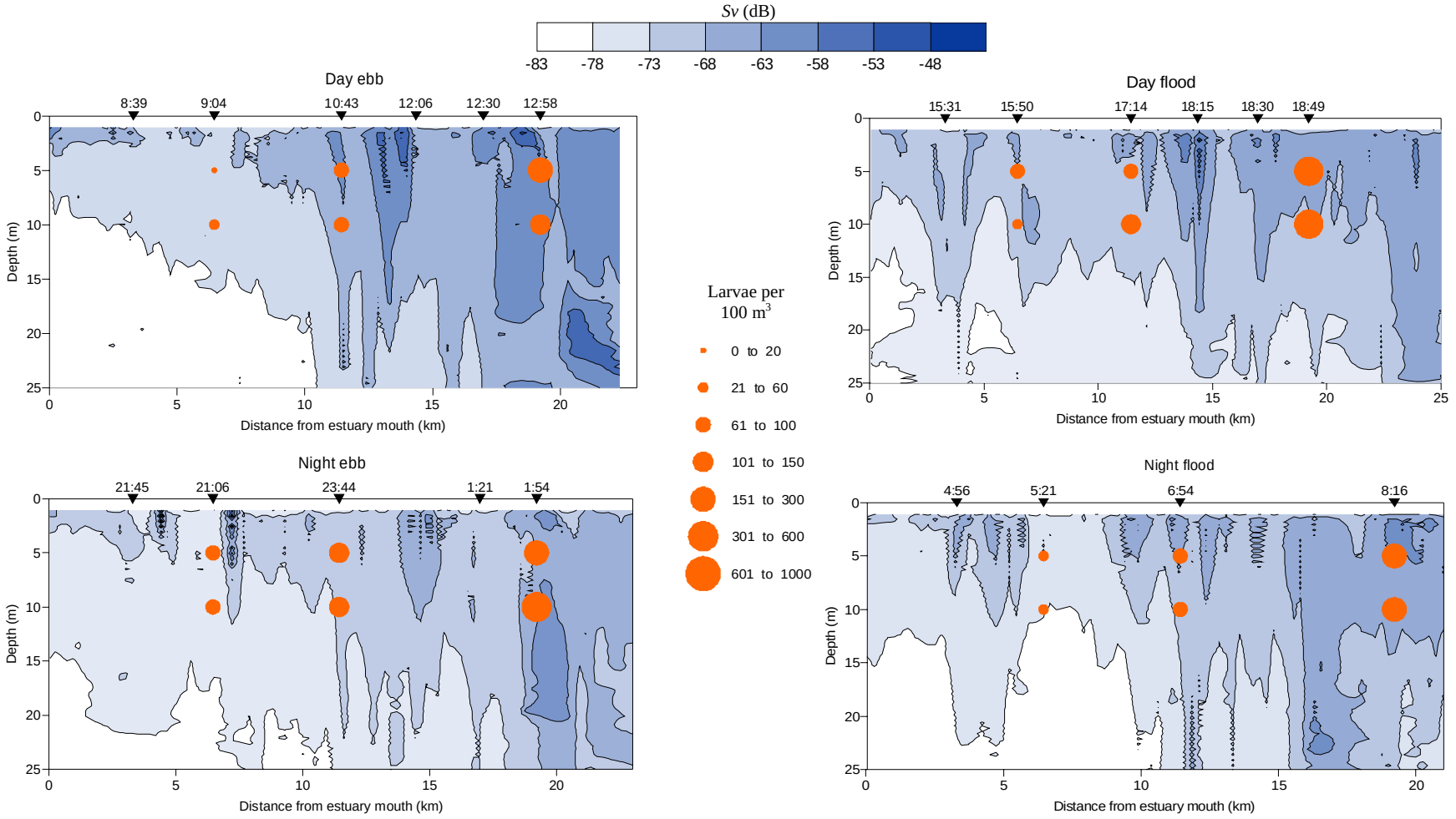

Figure 5.7. Vertical profiles of acoustic backscatter strength (dB) recorded along the entrance of the Tamar Estuary in December 2001 during two different tidal cycles. The mean larval fish concentrations (larvae/100 m^3) have been superimposed for each site and sampling time at the midpoint of the 0-10 m and 10-20 m depth strata (orange circles). Sampling time indicated at the top of each profile corresponds to East Australian Summer Standard Time.

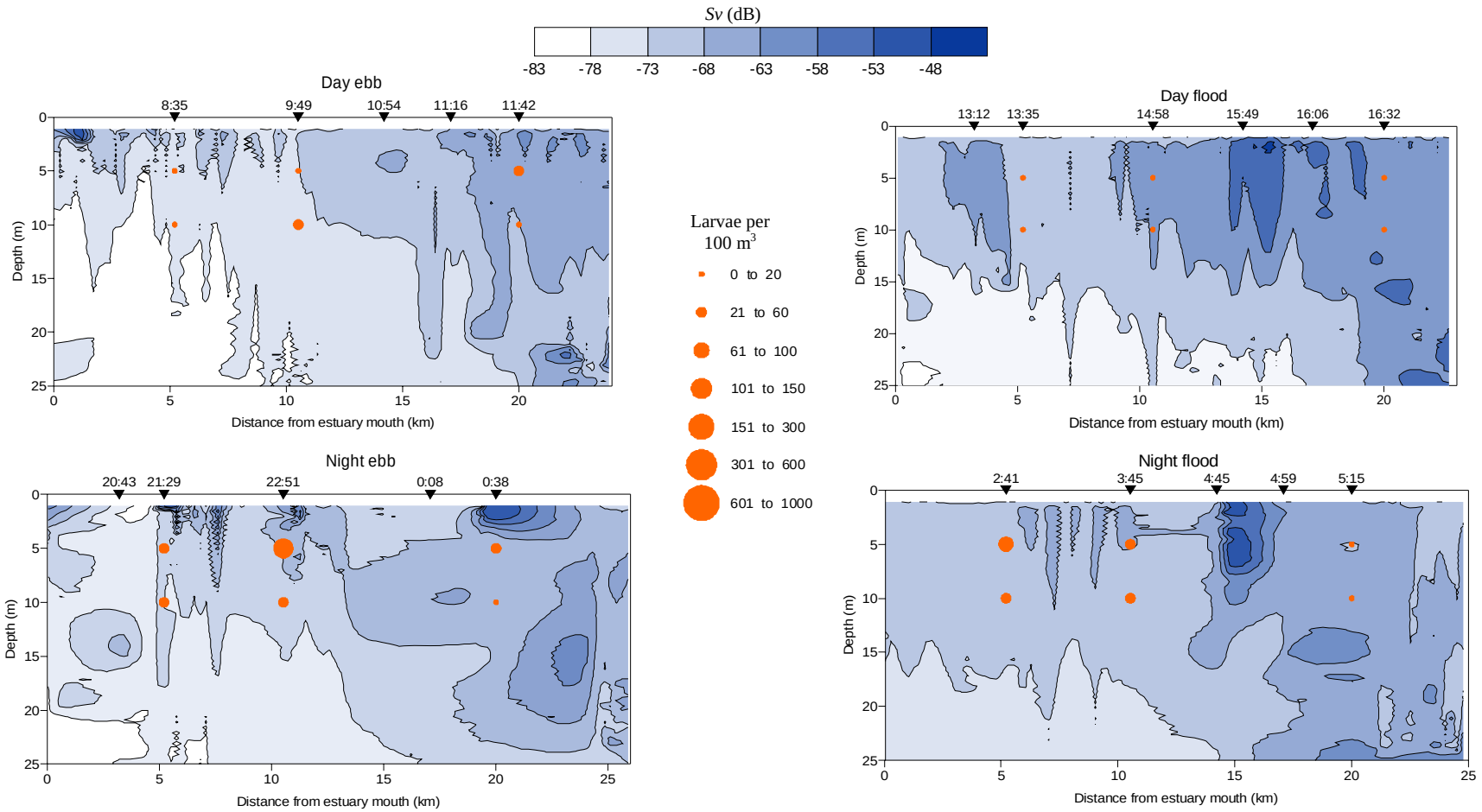

Figure 5.8. Vertical profiles of acoustic backscatter strength (dB) recorded along the entrance of the Tamar Estuary in January 2002 during two different tidal cycles. The mean larval fish concentrations (larvae/100 m^3) have been superimposed for each site and sampling time at the midpoint of the 0-10 m and 10-20 m depth strata (orange circles). Sampling time indicated at the top of each profile corresponds to East Australian Summer Standard Time.

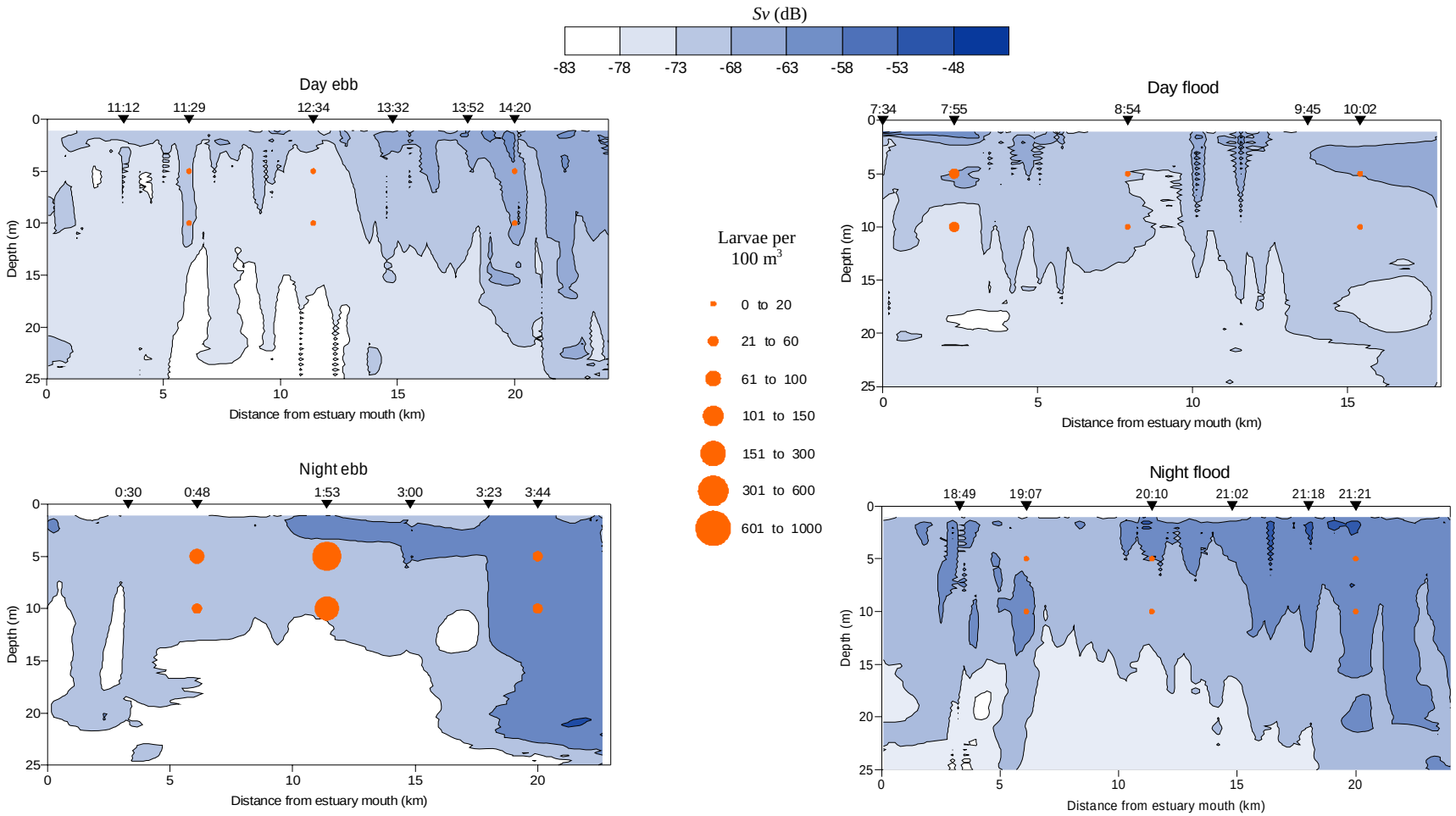

Figure 5.9. Vertical profiles of acoustic backscatter strength (dB) recorded along the entrance of the Tamar Estuary in February 2002 during 2 different tidal cycles. The mean larval fish concentrations (larvae/100 m^3) have been superimposed for each site and sampling time at the midpoint of the 0-10 m and 10-20 m depth strata (orange circles). Sampling time indicated at the top of each profile corresponds to East Australian Summer Standard Time.

5.4.5 Diel and tidal variation of abundant families

High concentrations of gobiids were recorded during flood tides and night ebb in December 2001, at night time in January 2002, and night ebb in February 2002 (Fig. 5.10). The spatial distribution of larval gobiids also differed by month, being higher at site 6 in December 2001, and becoming increasingly abundant downstream at sites 3 and 2 in January and February 2002. Visual inspection of larval gobiids showed mostly preflexion larvae in December 2001 and postflexion larvae in January and February 2002. Mean concentrations of gobiid larvae differed significantly with month, tide and site, with significant interactions (P<0.01) (Table 5.4).

Larval blenniids (*P. tasmanianus*) appeared to be more abundant during ebb tides in all months, with higher concentrations in December 2001. While a weak diel pattern was observed during January 2002, larval blenniid concentrations were always higher during ebb than flood tides (Fig. 5.11). Mean concentrations of blenniid larvae differed significantly by month and tide, with a significant interaction between sites and tide (P<0.01) (Table 5.4).

Mean concentrations of larval clinids differed significantly by month and site (P<0.001), with higher concentrations obtained in December 2001 and in sites 2 and 3 (Table 5.4, Fig. 5.10). Although there was a clear along estuary distribution in clinid concentrations, no diel or tidal patterns were observed.

Table 5.4 Results of multi-factorial ANOVA (ln-transformed data) for larval fish concentrations (larvae/100 m^3) of abundant families by month, tide and site. Tukey tests were performed when the effect of the factor was significant and no significant interaction between the factors. Abbreviations: D, December; J, January; F, February; NS, not significant; ***P*<0.01, ****P*<0.001.

	SS	df	MS	F	*P*	Tukey test
Gobiidae						
Month	112.98	2	56.49	304.37	***	
Tide	88.18	3	29.39	158.38	***	
Site	3.35	2	1.67	9.02	**	
Month x Tide	44.47	6	7.41	39.93	***	
Month x Site	41.98	4	10.49	56.55	***	
Tide x Site	6.61	6	1.10	5.93	***	
Month x Tide x Site	11.68	12	0.97	5.25	***	
Error	6.68	36	0.19			
Parablennius tasmanianus						
Month	13.94	2	6.97	7.84	**	D J F
Tide	15.55	3	5.18	5.83	**	
Site	1.16	2	0.58	0.65	NS	
Month x Tide	10.92	6	1.82	2.05	NS	
Month x Site	1.81	4	0.45	0.51	NS	
Tide x Site	19.16	6	3.19	3.59	**	
Month x Tide x Site	11.41	12	0.95	1.07	NS	
Error	31.99	36	0.89			
Clinidae						
Month	55.60	2	27.80	44.20	***	D J F
Tide	4.54	3	1.51	2.40	NS	
Site	37.22	2	18.61	29.58	***	2 3 6
Month x Tide	3.83	6	0.64	1.01	NS	
Month x Site	6.00	4	1.50	2.38	NS	
Tide x Site	3.67	6	0.61	0.97	NS	
Month x Tide x Site	5.03	12	0.42	0.67	NS	
Error	22.64	36	0.63			
Engraulis australis						
Month	20.58	2	10.29	40.15	***	
Tide	21.68	3	7.23	28.20	***	
Site	0.80	2	0.40	1.57	NS	
Month x Tide	9.62	6	1.60	6.26	**	
Month x Site	1.85	4	0.46	1.81	NS	
Tide x Site	1.78	6	0.30	1.16	NS	
Month x Tide x Site	2.63	12	0.22	0.85	NS	
Error	9.23	36	0.26			

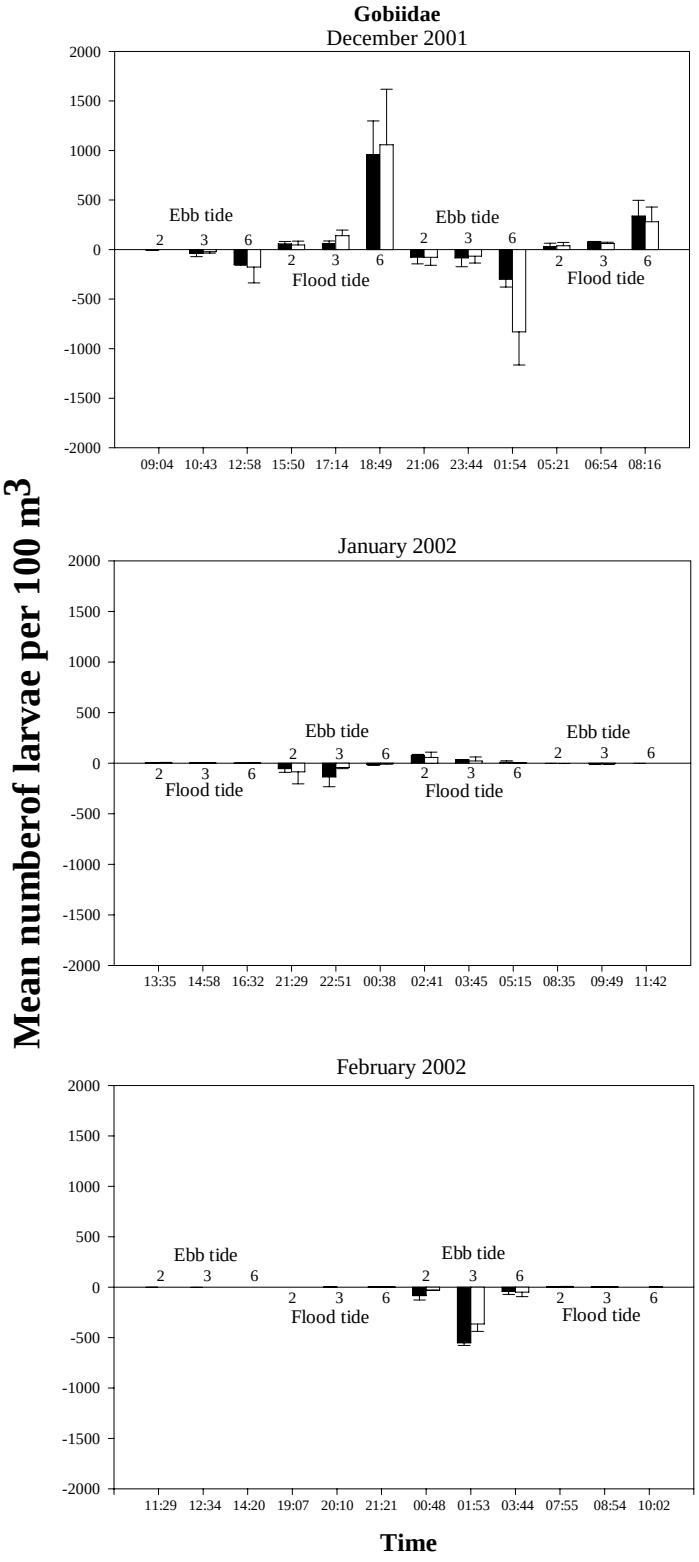

Figure 5.10. Mean (+95 C.I.) larval gobiid concentrations (larvae/100 m^3) during consecutive tidal cycles along the lower Tamar Estuary between December 2001 and February 2002. Numbers above and below bars indicate the sampling site. Time along the x-axis correspond to Eastern Australian Summer Standard Time. Black bars = 0-10 m depth stratum and white bars = 10-20 m depth stratum.

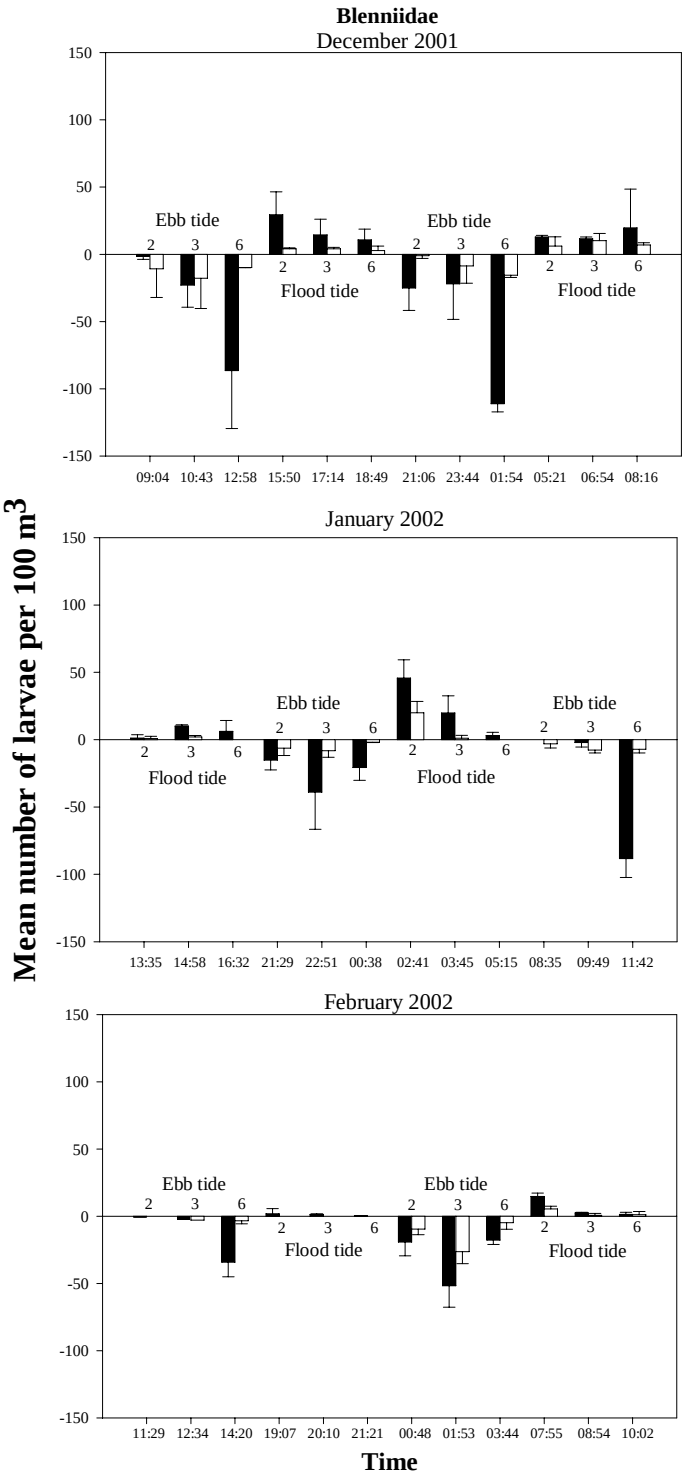

Figure 5.11. Mean (+95 C.I.) larval blenniids (*P. tasmanianus*) concentrations (larvae/100 m^3) during consecutive tidal cycles along the lower Tamar Estuary between December 2001 and February 2002. Numbers above and below bars indicate the sampling site. Time along the x-axis correspond to Eastern Australian Summer Standard Time. Black bars = 0-10 m depth stratum and white bars = 10-20 m depth stratum.

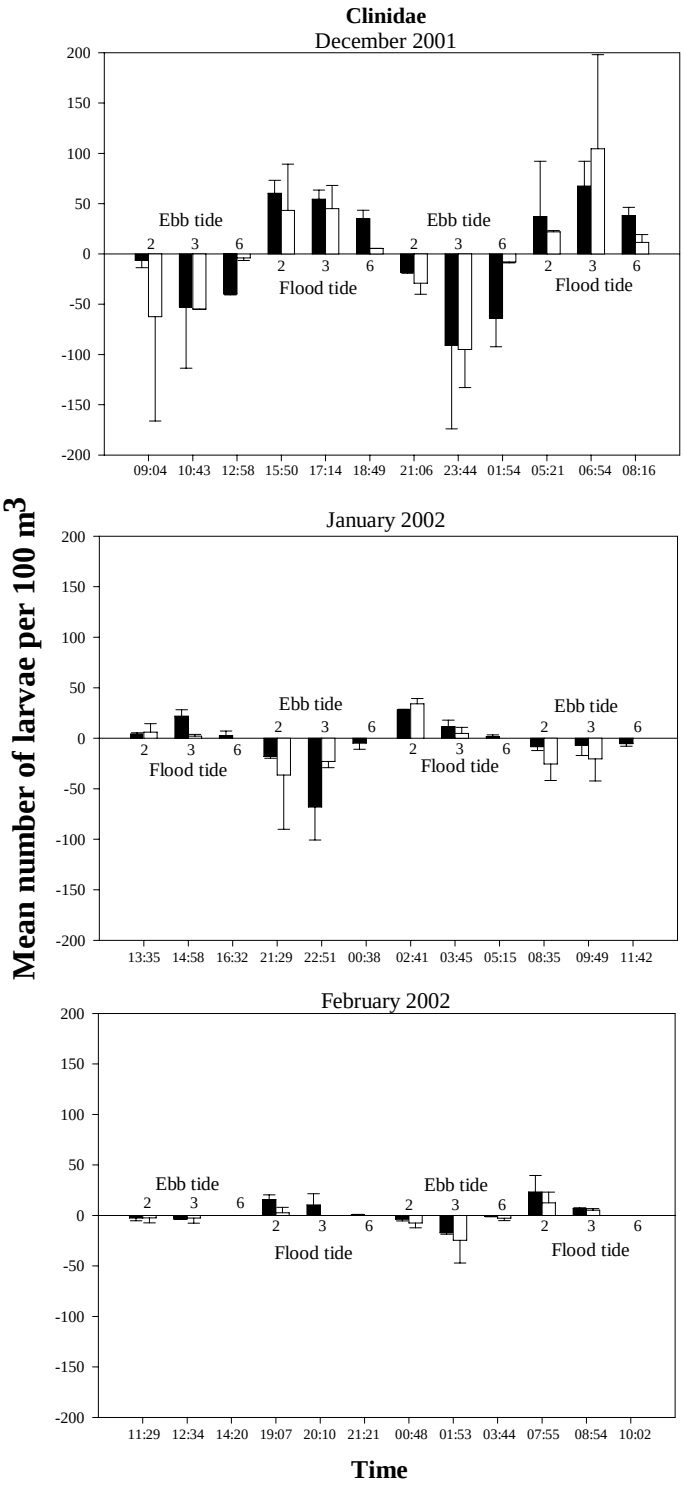

Figure 5.12. Mean (+95 C.I.) larval clinid concentrations (larvae/100 m^3) during consecutive tidal cycles along the lower Tamar Estuary between December 2001 and February 2002. Numbers above and below bars indicate the sampling site. Time along the x-axis correspond to Eastern Australian Summer Standard Time. Black bars = 0-10 m depth stratum and white bars = 10-20 m depth stratum.

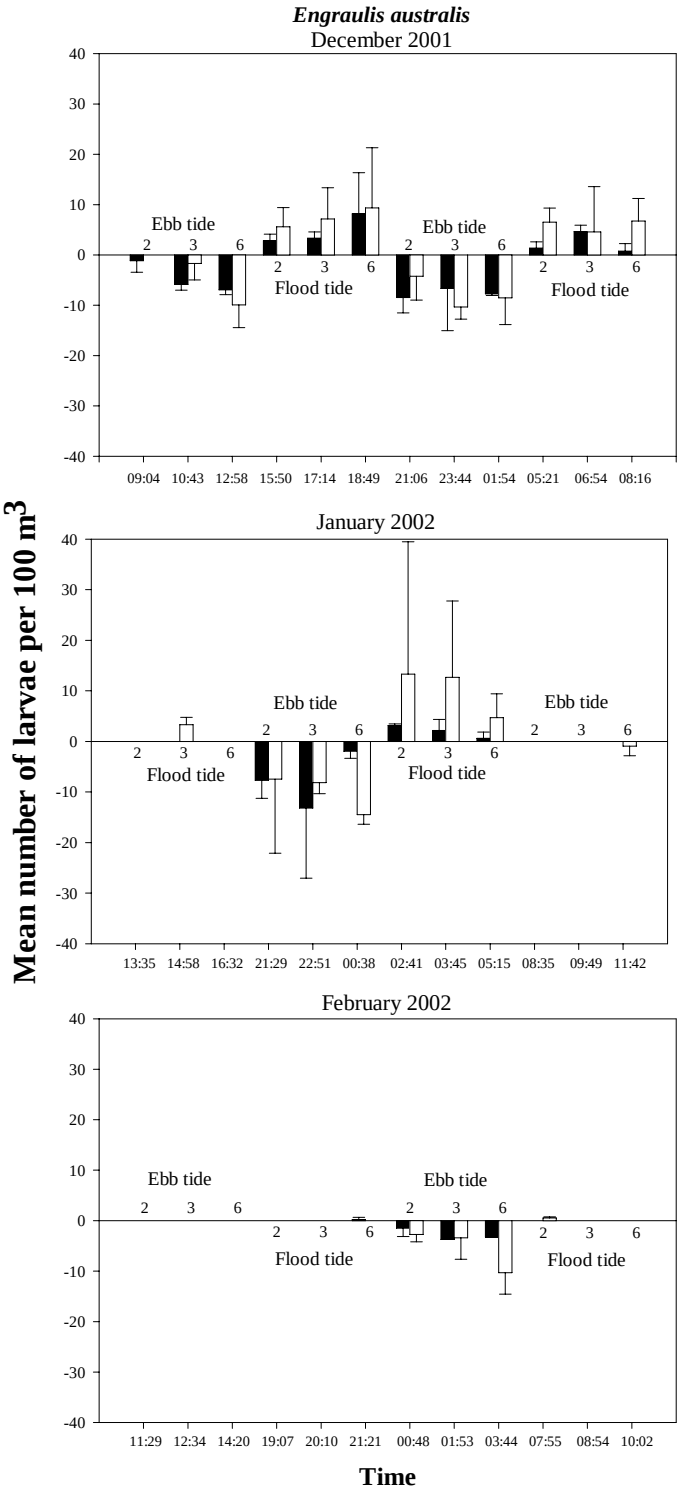

Figure 5.13. Mean (+95 C.I.) larval anchovy (*E. australis*) concentrations (larvae/100 m^3) during consecutive tidal cycles along the lower Tamar Estuary between December 2001 and February 2002. Numbers above and below bars indicate sampling site. Time along the x-axis correspond to the Eastern Australian Summer Standard Time. Black bars = 0-10 m depth stratum and white bars = 10-20 m depth stratum.

No clear along estuary, tidal or diel pattern in the distribution of anchovy concentrations were observed in December 2001 (Fig. 5.13). By contrast, a diel pattern was observed in January 2002 with higher concentrations during night time, whereas diel and tidal patterns were observed in February 2002, with high concentrations during night ebb. Unlike the other three families, most larval anchovy were caught in the 10-20 m stratum in all months. Mean concentrations of larval anchovy differed significantly by month and tide, with a significant interaction between them ($P<0.01$) (Table 5.4).

5.4.6 Diel and tidal variation in the larval fish assemblages

Classification and ordination of samples obtained at different tides and months, based on mean larval fish concentrations of 35 fish families, clearly distinguished three groups ($P<0.001$) (Table 5.5; Fig. 5.14a). Samples from December 2002, and night tide samples from January and February 2002 clustered into one group (Group 1) at >60% similarity, while day tide samples from January and February 2002, and night flood samples from February 2002 clustered into another group at ≥60% (Group 2). Day ebb samples from February 2002 did not cluster with any group (Group 3) (Fig. 5.14a). Non-parametric multidimensional scaling (NMDS) ordination supported the classification (Fig. 5.14b).

Differences in the concentrations of larval gobiids, blenniids and clinids were responsible for the groupings separated by the classification and NMDS ordination analyses. The presence of larval gobiesocids and anchovy in Group 1, and of larval syngnathids and monacanthids in Group 2, were also important factors in the

groupings (Table 5.6). A very high concentration of larval blenniids during day ebb in February 2002 was the main factor that separated it from the other two groups.

Table 5.5. Analyses of similarities (ANOSIM) a) between sample groups (mean larval fish concentrations) formed by classification and NMDS ordination analyses; and b) spatial differences of samples within each group. Global R indicates the level of difference between the different groups; 0 (indistinguishable) to 1 (different). ****P*<0.001

	a) Temporal	b) Spatial		
	MDS Groups	**Group 1**	**Group 2**	**Group 3**
Global R	0.99	0.88	0.81	0.85
P	***	***	***	***

Table 5.6. Percentage similarity (SIMPER) within Groups 1 and 2, showing the main taxa, respective mean concentrations (no. larvae/100 m^3) and cumulative contribution (%) of the most important families in Group 1 and 2.

Similarity within sample group (%)	Family	Mean concentration	Cumulative contribution (%)
Group 1 (71.8%)			
	Gobiidae	1008.9	32.9
	Clinidae	194.8	49.9
	Blenniidae	110.8	64.0
	Gobiesocidae	55.4	73.1
	Engraulidae	35.3	81.4
Group 2 (65.4%)			
65.4	Clinidae	45.1	31.9
	Blenniidae	39.6	49.4
	Gobiidae	9.7	64.2
	Monacanthidae	8.1	75.5
	Syngnathidae	4.6	83.3

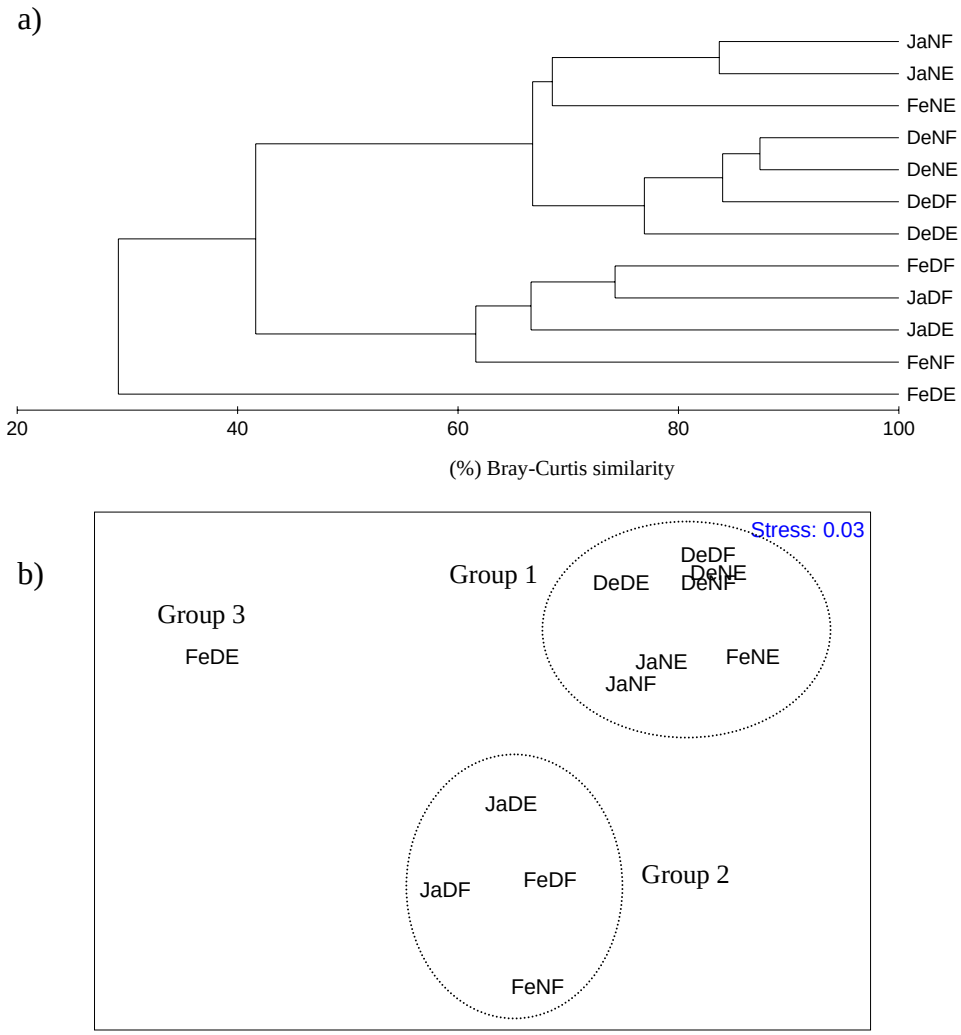

Figure 5.14. a) Group average classification and b) non-parametric multidimensional scaling (NMDS) ordination of samples (mean larval fish concentrations by family, larvae/100 m^3) taken at four different tides along the lower Tamar Estuary between December 2001 and February 2002. Abbreviations: De = December 2001, Ja = January 2002 and Fe = February 2002; last two letters DE = day ebb, NE= night ebb, DF = day flood, NF = night flood.

5.5 Discussion

Number of families differed primarily with diel cycles and secondarily with tidal cycles, with larvae of 21 families more abundant during night than during day time, eight of which were caught exclusively during the night. A tidal pattern was observed

in 13 families only, with seven caught exclusively during ebb tide and one during flood tide. This implies a stronger influence of diel than tidal cycles in the occurrence of larval fishes in the water column. Families caught exclusively during either one tide or time (day/night) were usually represented by a small number of larvae, and sometimes only by one larva, as in the case of the Ophidiidae, Myctophidae and Serranidae. The incidental presence of larvae of marine taxa in the lower Tamar Estuary during ebb tides suggests that they may have been swept into the estuary by the strong flood currents and have become temporarily trapped in a plug of tidal water (Melville-Smith *et al.*, 1981; Beckley, 1985; Trnski, 2001). This incidental advection of marine taxa (i.e. Leptoscopidae, Triglidae, Gempylidae) from outside the estuary has also been reported in many estuaries both in temperate Australia and overseas (Melville-Smith *et al.*, 1981; Beckley, 1985; Miskiewicz, 1986; Steffe, 1991; Neira and Potter, 1992a,b, 1994; Hannan and Williams, 1998; Joyeux, 1999; Trnski, 2001).

Mean concentrations of larval fishes varied with tide and time, but exhibited a stronger diel pattern in most months. That is, they were more abundant during the night than during the day. Two main reasons for the observed diel pattern in concentrations are net avoidance and/or diel vertical migration. While concentration of larval fishes from plankton nets closely corresponded to the acoustic backscatter strength (*Sv*) recoded by the ADCP during December 2001, there was a lack of correspondence between concentrations and *Sv* in the two subsequent months, with low larval concentrations obtained where high *Sv* were recorded. Visual inspection of larval fishes caught during February 2002 showed that most were at the postflexion stage, while those caught in December 2001 were mainly preflexion. The presence of very few, mostly postflexion larvae in February 2002 during day sampling suggests

the possibility of a significant net avoidance, as larvae are more likely to avoid the net at this and older stages (Fortier and Leggett, 1982; Tzeng and Wang, 1993; Harris *et al.*, 1999). However, greater larval fish concentrations were obtained during night ebb than during night flood in February 2002, indicating that although net avoidance may play a role in the observed diel pattern, behaviour such as vertical migration may also be important.

The stronger diel than tidal pattern in the concentrations of the majority of the larval fishes in the Tamar Estuary contrasts that found in estuaries and enclosed bays in temperate Australia and South Africa, including Wilson Inlet, Botany Bay, Lake Macquarie and the Sundays River Estuary, where tidal phase was found to be the major factor influencing larval fish concentrations. However, most of these systems are either wave-dominated with low flow velocities compared to those in the Tamar Estuary (~2 m/s), or have a two-layered circulation flow (Melville-Smith *et al.*, 1981; Miskiewicz, 1986; Steffe, 1991; Neira and Potter, 1992a; Kingsford and Suthers, 1996; Hannan and Williams, 1998; Harris and O'Brien, 1998). Similar to the findings of this study, a stronger diel than tidal variation in larval fish concentrations has been documented in estuaries or sections of estuaries with weak or no vertical stratification, and/or with strong tidal currents (>1 m/s), such as Swansea Channel in Australia, Swartvlei Estuary in South Africa, Whangateau Harbour in New Zealand and Beaufort Inlet in United States (Roper, 1986; Whitfield, 1989a; Churchill *et al.*, 1999; Forward Jr *et al.*, 1999; Trnski, 2001). This in turn supports the view that behaviour and retention mechanisms employed by larvae may depend on the prevalent hydrographic features of individual estuaries (Weinstein *et al.*, 1980; Fortier and Leggett, 1982; Grioche *et al.*, 1999; Grioche *et al.*, 2000; Hare *et al.*, 2005).

The high concentrations of early-stage gobiid larvae caught at upstream site 6 in December 2001 suggests that the majority of these larvae were spawned within the estuary. The early stage of these larvae, combined with the strong tidal currents (see Chapter 2 for details), may have been responsible for the lack of tidal or diel pattern in concentrations observed during December 2001. The lack of pattern is likely due to larvae behaving mostly like passive particles, given their poor swimming ability at that stage (Roper, 1986; Forward Jr *et al.*, 1999). Concentrations of larval gobiids showed a diel pattern in January 2002, and diel and tidal patterns in February 2002, at the time when larger amounts of postflexion gobiid larvae were collected. This suggests a change in behaviour in terms of swimming ability, with vertical migrations and/or net avoidance taking place.

Concentrations of larval anchovy (*E. australis*) were usually greater in the 10-20 stratum during all tidal cycles and months, with larvae displaying diel and/or tidal patterns in January and February 2002. The vertical distribution of larval anchovy in the lower Tamar Estuary parallels that of larvae of other anchovy species in estuaries in United States (Schultz *et al.*, 2003). In traditional estuaries, i.e. those with two-layered circulation, such behaviour aids upstream transport (Weinstein *et al.*, 1980; Whitfield, 1999). However, in the absence of such circulation in the Tamar Estuary, the only plausible explanation of why anchovy larvae may prefer deep layers is to avoid the stronger surface currents and hence loss from the system. In fact, most anchovy larvae collected in this study were already at the flexion or postflexion stage, which suggests an improvement in their swimming ability and thus their capacity to maintain their vertical position. The increase in their swimming ability is supported

by Raudzens (2002) who reported tidal and diel patterns displayed by postflexion larval anchovy caught in April 2001 at the entrance of the Tamar Estuary. Although the tidal pattern differed from this study, with greater concentrations of larval anchovy found during night flood instead of night ebb tide, it suggests that tidal and diel variations in the distribution of larvae may take place until larvae are more developed and their swimming ability has improved.

Larvae of the blenniid *Parablennius tasmanianus* were the only ones to display a tidal pattern in the Tamar Estuary, with higher concentrations during ebb tides. High concentrations of blenniid larvae as well as gobiids, have been reported being passively swept out of estuaries during ebb tides in Western Australia, South African and New Zealand estuaries (Beckley, 1985, 1986; Roper, 1986; Whitfield, 1989a,b; Neira and Potter, 1992a). This has led to the establishment of a fourth life history category, namely resident estuarine species that spawn in the estuary, and whose preflexion larvae leave the system on the ebb tide and return at the postlarval stage (Whitfield, 1989a). Neither postflexion or settlement stages of blenniids were recorded in this study, perhaps because they could be concentrating along the estuary banks, or in deeper waters where flow velocities are considerably lower, and where sampling could not be conducted.

Larval clinids did not exhibit any evidence of tidal or diel pattern during the study. However, clinid larvae showed a strong along-estuary pattern with decreasing concentrations from downstream site 2 to upstream site 6. The lack of tidal or diel pattern exhibited by clinid larvae could be due to a number of factors, including the presence of different species displaying different species-specific behavioural

mechanisms (Weinstein *et al.*, 1980; Boehlert and Mundy, 1988; Epifanio, 1988; Shaw *et al.*, 1988; Norcross, 1991). On the other hand, the spatial distribution of clinid larvae could be reflecting the distribution of the adult populations, and possibly localized spawning in rocky and weedy reef areas along the entrance of the Tamar Estuary (Last *et al.*, 1983; Gomon *et al.*, 1994; Jordan *et al.*, 1998; Edgar *et al.*, 1999).

Results from this study indicate that the hydrodynamic characteristics of the Tamar Estuary may increase the chances of larval fishes being advected out of the estuary. This in turn may trigger the adoption of retention mechanisms other than selective tidal transport to remain inside the estuary, such as remaining near the bottom and/or along the banks where current velocity is slower (Johnson and Gonor, 1982; Boehlert and Mundy, 1988). The adoption of alternative retention mechanisms could, for example, explain the low abundance of larval atherinids caught in the Tamar Estuary during this study compared to other temperate estuaries in Australia (Gaughan *et al.*, 1990; Neira *et al.*, 1992; Neira and Potter, 1992b, 1994; Newton, 1996; Hannan and Williams, 1998). Instead, very high abundances of larval and juvenile atherinids have been caught along several sites in the lower Tamar Estuary, suggesting that atherinids may be selecting those low-velocity areas to avoid being flushed out of the estuary (Neira and Lara, in prep). Another mechanism that could be important to avoid being flushed out of the estuary is rapid settlement, as it has been suggested to occur with larval gobiids and young flounder in Whangateau Harbour (New Zealand) where tidal velocities exceed 1.5 m/s (Roper, 1986). While this could also be applied to larval gobiids in the Tamar Estuary, sampling of newly-settled gobiids during this study was not possible given the irregular bathymetry of the system and the strong tidal currents.

There are several fish species that are found in the Tamar Estuary and whose larvae were found in small numbers or not found at all during this study, including sand flathead, Australian salmon, yellow eye mullet and slimy cod (Jordan *et al.*, 1998). It is likely that larvae from these species are not being recruited into the system as larvae and are instead entering as juveniles.

The strong tidal currents, characteristic of the Tamar Estuary, coupled with the lack of two-layered circulation, may be the factors determining the stronger diel than tidal patterns in larval fish concentrations. In addition, the hydrodynamic characteristics of the estuary may be influencing the distribution of the larval fish assemblage by favouring larvae from species with the appropriate adaptations, such as demersal eggs, high fecundity and parental care, while larvae of other estuarine-dependent species may be entering at a later stage and/or along the banks to avoid the strong tidal currents, or are spawned in areas far from the estuary mouth.

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Chapter 6

Simulated transport of larval fishes through the lower Tamar Estuary using a 1-dimensional model

6.1 Abstract

Simulated concentrations of "passive" particles predicted by a 1-dimensional estuarine transport model were compared to overall larval fish concentrations obtained during three 24-hour sampling sessions in the lower Tamar Estuary between December 2001 and February 2002, and those of the most abundant families. The Tamar Estuary was divided into segments, with segment 1 corresponding to Bass Strait and segment 6 corresponding to the uppermost section of the lower estuary. In general, the model used explained ~94% of the variance in concentrations of all larvae, with simulated concentrations differing by ~24% from field-obtained concentrations. The greatest correspondence between simulated and field-obtained concentrations was found in segment 2 whereas the weakest occurred in segment 3, both during February 2002. The model explained >70% of the variance in larval concentrations of Gobiidae, *Parablennius tasmanicus*, Clinidae and *Engraulis australis*, with simulated and field-obtained concentrations differing by <55%. In order for simulated concentrations to match field-obtained concentrations, the boundary conditions in segment 1 were set following observed concentrations, while an exponential decrease model in particle load representing larval production rate was used for segment 6. The close match between simulated concentrations of "passive" larvae and field-obtained larval concentrations indicates that the representation of the larval production rate and its decay time was a reasonable estimate for the Tamar Estuary. The 1-dimensional

model utilized was deemed as sufficient to give a general overview of the influence that circulation has on the distribution of larvae and of the larval production in the estuary. Despite these findings, larval transport estimates could be improved if lateral and vertical differences in advection and diffusion as well as the vertical migration of larvae are considered in future models.

6.2 Introduction

The importance of larval supply in determining the structure of many marine populations has been long established (Doherty and Williams, 1988; Roughgarden *et al.*, 1988; Jenkins and Black, 1994; Brown *et al.*, 2000, 2004). For fish species with estuarine-dependent larvae, the timing in the transport of these stages to suitable settlement areas inside estuaries is crucial to ensure recruitment success. The net seaward transport of larvae by currents is responsible for substantial larval mortality and subsequent recruitment failure (Jackson and Strathmann, 1981; Jenkins and Black, 1994; Brown *et al.*, 2004). In this context, passive and active mechanisms to enter and remain within estuaries are employed by several larval fishes to increase their chances of reaching suitable estuarine settlement areas (Weinstein *et al.*, 1980; Fortier and Leggett, 1983; Norcross and Shaw, 1984; Boehlert and Mundy, 1988; Forward Jr *et al.*, 1999; Schultz *et al.*, 2000, 2003; Trnski, 2001). The study of these mechanisms have represented a challenge for both biologists and oceanographers, given the difficulties in gathering data in the appropriate time and space scales to detect the response of larvae to estuarine circulation (Boicourt, 1982). On the other hand, attempts to correlate larval abundances with environmental factors have been

unsuccessful due to the complexity of the dominant physical processes involved in the recruitment and retention of larvae within estuaries (Jenkins and Black, 1994; Dixon *et al.*, 1999; Brown *et al.*, 2004). However, since larval transport depends on a time series of events rather than the presence or absence of single factors, the utilization of numerical transport models offers an alternative approach to analyse the mechanisms influencing larval transport into early nursery areas within estuaries (Hermann *et al.*, 1996; van der Veer *et al.*, 1998; Werner *et al.*, 1999; Brown *et al.*, 2004).

The advantage of transport simulations is that they are not affected by sampling limitations or behaviour, and allow the incorporation of complex non-linear processes occurring at different time and spatial scales (Brown *et al.*, 2004). Several transport models have been applied to simulate the transport of larvae from different organisms within estuaries, including larval fishes, starfishes and abalone. One of the models that has been successfully used to predict larval distributions relies on the assumption that larvae behave as passive particles, i.e. early larval stages are unable to swim horizontally and hence overcome strong tidal currents. (Fortier and Leggett, 1982; de Lafontaine *et al.*, 1984; Jenkins and Black, 1994; Blanton *et al.*, 1999; Brown *et al.*, 2000, 2004). This chapter predicts larval fish concentrations along the lower Tamar Estuary using a simple (1-dimensional) estuarine transport model that assumes larvae behave as passive particles and compares these values with field-obtained concentrations. The advantage of employing numerical models to study larval fish transport is discussed.

6.3 Materials and methods

6.3.1 Field data

Field-obtained larval fish distribution were derived from three 24-hour sampling sessions carried out during ebb and flood tides between December 2001 and February 2002 along the lower Tamar Estuary (see Chapter 5 for details). Daily freshwater flow data from the North and South Esk rivers between November 2001 and February 2002 were provided by the Australian Bureau of Meteorology and Hydro Tasmania, respectively. Salinity data and larval fish concentrations (larvae/m^3) were averaged for each site over an entire 24-hour cycle (~2 tidal cycles), whereas river flows from both tributaries were averaged for the seven days preceding each 24-hour sampling session.

6.3.2 Transport model

The transport section of the Simple Estuarine Eutrophication Model (SEEM) was used to simulate larval fish transport within the lower Tamar Estuary (Parslow *et al.*, 1999). The model has two components: an **inverse model** to estimate volume exchanges (m^3/s) between the different segments of the estuary, and an **n-layered transport model** which divides the estuary length-wise into "m" columns and vertically into "n" layers, and allows two-way vertical and horizontal exchanges representing both advection and diffusion. In order to run the n-layered transport model it is necessary firstly to run the inverse model. In the absence of a two-layered circulation in the Tamar Estuary (see Chapter 2 for details) the model assumed

circulation along one layer, and was used to simulate only particle transport in the lower section of the Tamar Estuary, i.e. within 20 km from the estuary mouth.

6.3.2.1 Inverse model

To drive the transport model, the physical exchanges (water volume and concentration fluxes) were estimated with an inverse technique that employs observed salinity fields, observed river flows and estuary geometry (Hunter, 1998). Two fluxes of water in opposite directions were calculated between cell faces, i.e. $\mathbf{q}_{i,i+1}$ and $\mathbf{q}_{i+1,i}$, where the flux is directed from the cell indicated by the first subscript to the cell indicated by the second subscript (Fig. 6.1). Using salt as a tracer, salt flux from cell *i* to cell *i+1* is given by:

$$\boldsymbol{S_i q_{i,i+1} - S_{i+1} q_{i+1,i} = 0} \qquad \text{(Eq. 1)}$$

and the total flux of water is given by:

$$\boldsymbol{q_{i,i+1} - q_{i+1,i} = R} \qquad \text{(Eq. 2)}$$

From Eq. 1 and 2, fluxes between cell faces are then calculated using the following equations:

$$\boldsymbol{q_{i,i+1} = R \frac{S_{i+1}}{S_{i+1} - S_i}} \qquad \text{(Eq. 3)}$$

$$\boldsymbol{q_{i+1,i} = R \frac{S_i}{S_{i+1} - S_i}} \qquad \text{(Eq. 4)}$$

where **R** is the river flow (m^3/s) and **S** the salinity (PSU), with subscripts indicating the cell horizontal index. The flux of a tracer to the right of the boundary between cell *i* and *i+1* is given by $\boldsymbol{C_i q_{i,i+1} - C_{i+1} q_{i+1,i}}$, where **C** is the tracer concentration (Fig. 6.1).

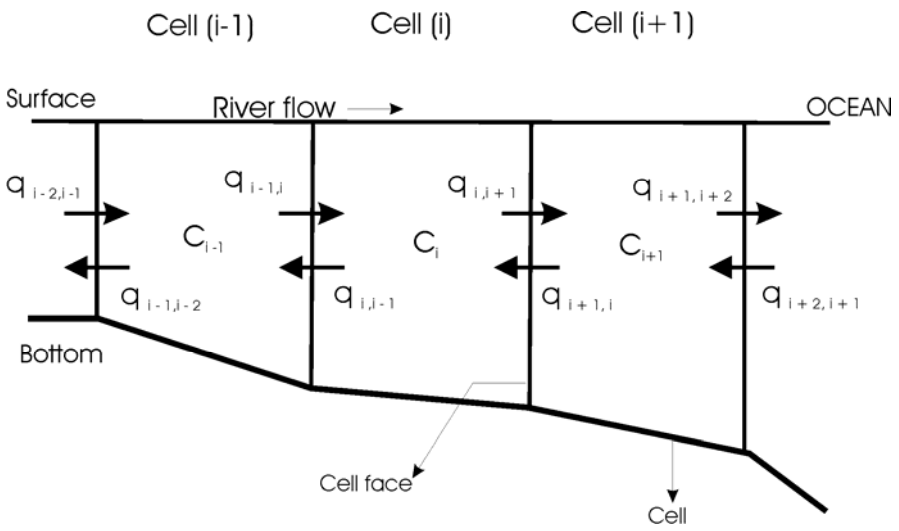

Figure 6.1. Diagram showing the exchange fluxes in a single layer model. Abbreviations: **C,** concentration of a tracer; **q** water fluxes through the cell faces; subscripts specify the position of the cell.

To run the inverse model, the estuary was divided into five different segments with a boundary segment at Bass Strait following the locations of each of the six fixed sites sampled during the 24-hour sessions (Fig. 6.2). The geometry of the estuary, i.e. surface area (m^2) and length (m) of each estuary segment was obtained using ArcView®; depth corresponded to the mean depth of the main channel. Average salinity data and river flow were also used to run this part of the model. For simplification, the term "segment" is used herein to refer to either model cells, estuary segments or sampling sites.

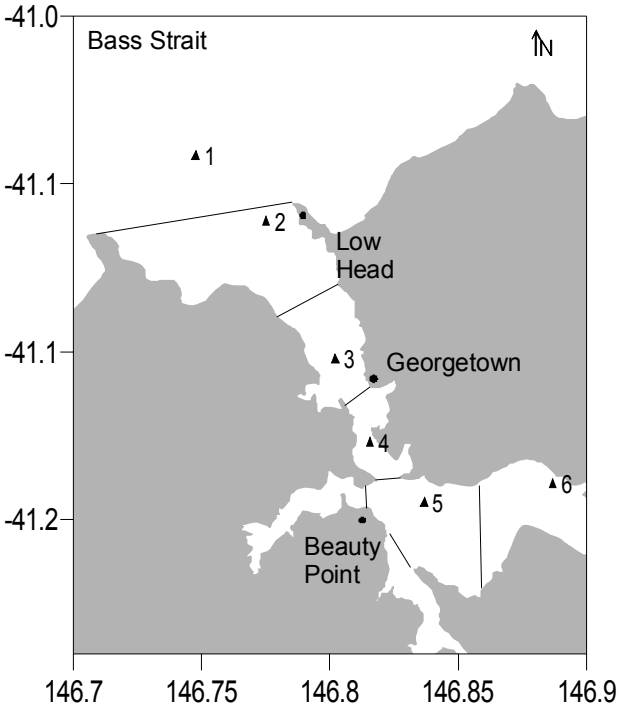

Figure 6.2. Map of the lower Tamar Estuary showing the five segments in which the estuary was divided, boundary segment (Bass Strait) and the location of the six fixed sites (▲) sampled in 24-hour sampling sessions carried out between December 2001 and February 2002.

6.3.2.2 1-layered model

This component of the transport model uses a river flow time series, the geometry of the estuary and the exchange fluxes between estuary segments, which were previously calculated with the inverse model to simulate transport of particles or pollutants within the estuary. The model requires three inputs: 1) initial conditions of tracer concentration in each segment; 2) boundary conditions (expressed as a time series) in the seaward segment (Bass Strait); and 3) tracer inputs (or loads, also expressed as time series) in all segments except Bass Strait.

The 1-layered model used daily time series of river flow data from the North and South Esk rivers recorded between November 2001 and February 2002. This model was run at 1-hour intervals providing outputs every 24 hours. Boundary conditions were set in segment 1 (Bass Strait), while the only load input was specified for the upstream-most segment 6 (Long Reach).

To calculate the flushing time (τ^f) of the estuary, initial tracer conditions were set to zero everywhere except segment 6, and both the boundary condition and loads were also set to zero. Results were plotted in MATLAB and an exponential equation was fitted to calculate τ^f.

To simulate larval fish transport, field-obtained concentrations from the 24-hour sampling sessions recorded in segment 2 (estuary entrance) were used to set the boundary condition in segment 1 (Bass Strait). Passive particles (larvae) were released into the model as a load (larvae/s) in segment 6 following an exponential decline representing a decline in larval production with time after the start of the spawning season (Fig. 6.3a). The release of these "passive" larvae into segment 6 started at t = 0, at a rate of 3500 larvae/s and an exponential decay time (τ^d) of ~5 days, i.e. the time in which the particle release (spawning) declines by 1/e. The release of particles in segment 6 and the exponential equation were determined following observed concentrations and distribution of larvae. Since the main spawning season started in November 2001 (see Chapter 4 for details), the model was run from that month until the end of February 2002, when the last 24-hour sampling session was carried out.

The model was also used to simulate the transport of larval fishes of the dominant families using the same approach. The release of "passive" larvae from gobiids and blenniids (*Parablennius tasmanicus*) were also set in segment 6 following the same exponential decline in time and the same τ^d (Fig. 6.3a), with initial concentrations of 3200 and 100 larvae/s at $t = 0$ for gobiids and blenniids, respectively. The release of "passive" anchovy larvae (*Engraulis australis*) was also set in segment 6, but with a τ^d of ~4 days and a starting input of 60 larvae/s (Fig. 6.3b). The input of "passive" larvae of gobiids, blenniids and anchovy in segment 6 was based on their higher concentrations obtained at that segment (Chapter 5), thus assuming that these larvae were spawned within or upstream of that region of the estuary. In the case of larval clinids, field-obtained concentrations were higher in segments 2 and 3, therefore only the boundary conditions in segment 1 were modified to simulate their distribution following field-obtained concentrations from segment 2, no loads were used for this simulation.

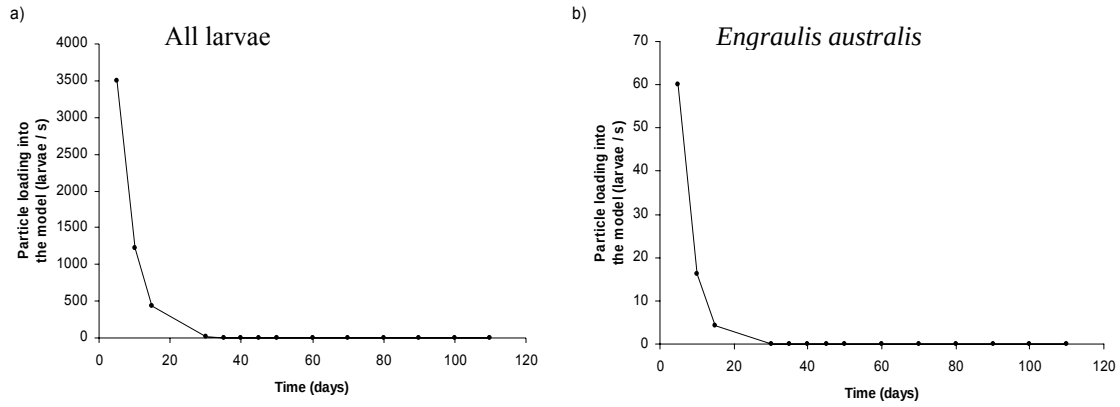

Figure 6.3. Simulated exponential particle loading (larvae/s) of a) all larvae combined and of b) *E. australis*, used for the model in segment 6 showing the decline in time after the start of the spawning season. Exponential equations used for particle input (loads) in segment 6 are: a) $y = 9968.1e^{-0.2093t}$ and b) $y = 223.66e^{-0.2632t}$, where **t** is time and $t = 0$ was set at the start of November 2001.

Values of release rates and of the exponential decaying times used for all larval fishes combined and for gobiids, blenniids and anchovy were chosen in order to improve the correspondence between the simulated and field-obtained larval fish concentrations.

6.3.3 *Data analyses*

Simulated larval concentrations of all families combined, and those of the four dominant families predicted for the 24-hour sampling sessions, were compared against their field-obtained concentrations. In order to estimate which percentage of the observed variability was explained by the model, the explained variance (**VE**) was calculated from the variance ratio between the variance of the residual values relative to the overall variance using the following equation:

$$VR = \frac{\sum_{1}^{n} (O - P)^2}{\sum_{1}^{n} O^2} \qquad \text{(Eq. 5)}$$

where **VR** is the variance ratio, O and P are the field-obtained and predicted concentrations respectively. From the above equation, $VE = 1 - VR$ and the standard deviation (**SD**) is $\sqrt{VR}$, n = 9. All of these factors were obtained per site and per month (n = 3) in order to estimate how the model performed depending on the location in the estuary and time of year.

6.4 Results

6.4.1 *Simulated concentrations*

Flushing time (τ^f) calculated from the simulated concentrations of a tracer placed in segment 6 showed an exponential decline in which the tracer concentration was reduced by 90% in 23 to 25 days flushing time (Fig. 6.4).

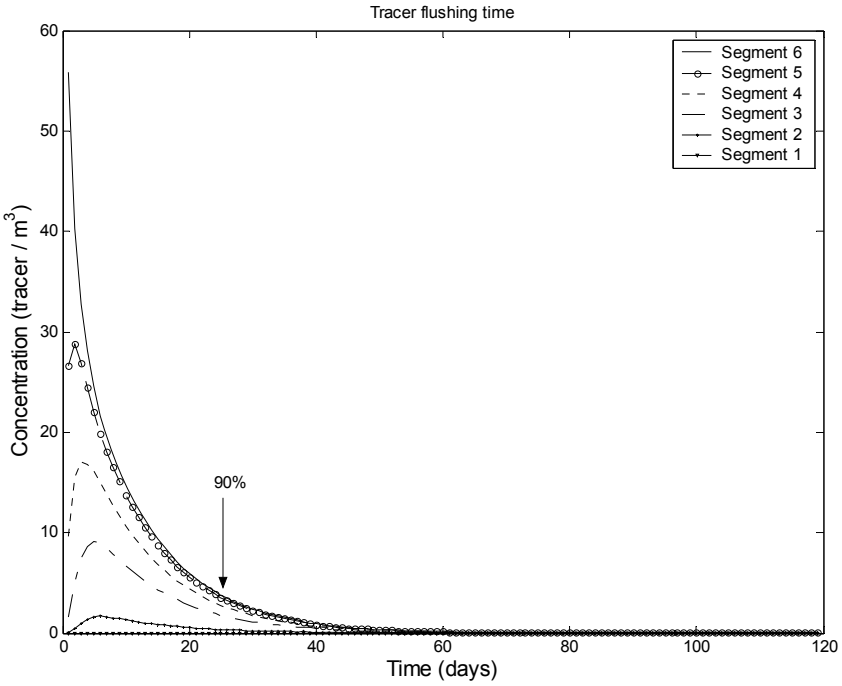

Figure 6.4. Simulated exponential decay in tracer concentration along the lower Tamar Estuary in the five different estuary segments; approximate time of 90% decline in concentrations (23-25 days) is also shown. The best fit exponential equation for the tracer concentration (***C***) at site 6 is $\boldsymbol{C = 45.2e^{-0.098t}}$, where *t* is time.

Changes in the simulated concentrations of "passive" larvae were greater in segment 6 and the adjacent segment 5 than at the downstream segments 2 and 3, with simulated concentrations reaching a peak in ~25 days before declining with a $\sim\tau^d = 30$ (Fig. 6.5).

While the simulated larval concentration reached a maxima of ~8 larvae/m^3 in segment 6, segment 2 reach a maxima of only <1.5 larvae/m^3.

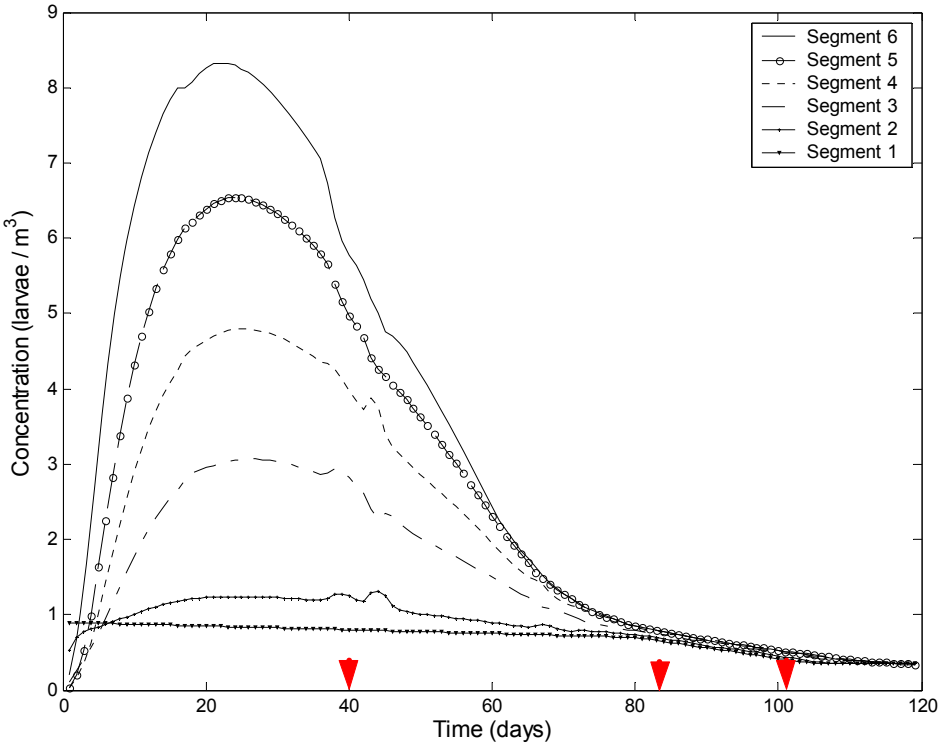

Figure 6.5. Daily trends of simulated concentrations of "passive" larval fishes in the five segments along the lower Tamar Estuary and in Bass Strait (segment 1), beginning at the start of November 2001 and finishing by the end of February 2002. Days when the 24-hour sampling sessions were carried out are indicated with red arrows.

Simulated concentrations in segment 6 peaked at 8.3 larvae/m^3 by day 22, and decreased to 5.8 larvae/m^3 by day 40 (first 24-hour sampling session) (Fig. 6.6). By day 40, simulated concentrations in segments 3 and 2 were 2.8 larvae/m^3 and 1.2 larvae/m^3, respectively. By day 84 (second 24-hour sampling session), simulated concentrations had declined to 0.8 larvae/m^3 in segment 6 and to 0.7 larvae/m^3 in segments 2 and 3, representing an 87% decline from the day 40 concentration. By day

102 (third 24-hour sampling session) concentrations at all segments had declined to ~0.5 larvae/m^3, representing a 97% decline from day 40 concentrations.

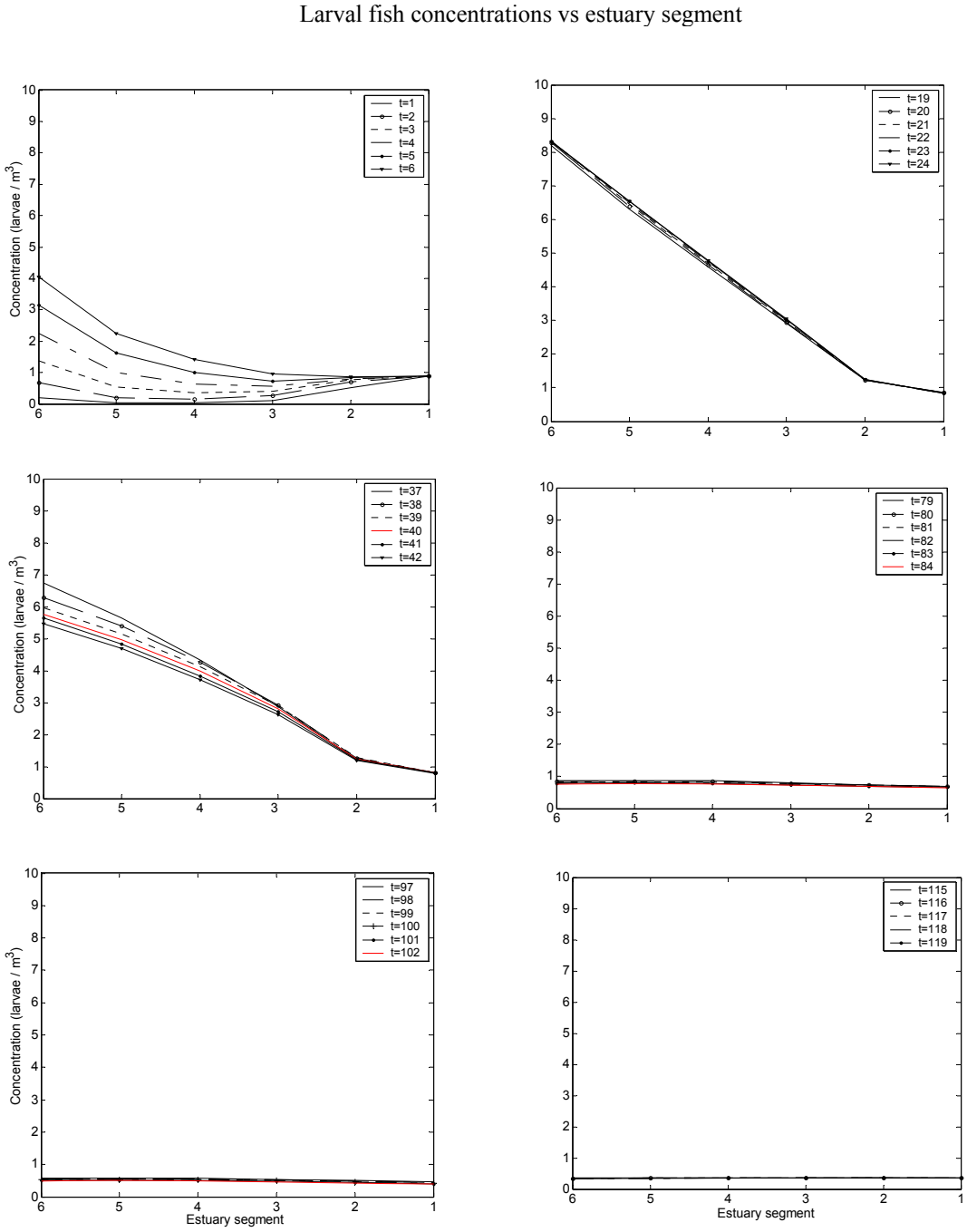

Figure 6.6. Changes in simulated concentrations of "passive" larval fishes in the different segments along the lower Tamar Estuary. Each plot shows the change in concentration on six consecutive days; t = day number. Simulated concentrations from the days when the 24-hour sampling session were carried out are indicated in red.

Simulated larval concentrations of gobiids, blenniids and anchovy reached a maxima in ~20 days, while larval clinid concentrations were highest at the beginning of the season (t = 1) (Fig. 6.7). Simulated concentrations of gobiids, blenniids and anchovy were greatest in segment 6, whereas clinid concentration was greatest in segment 2.

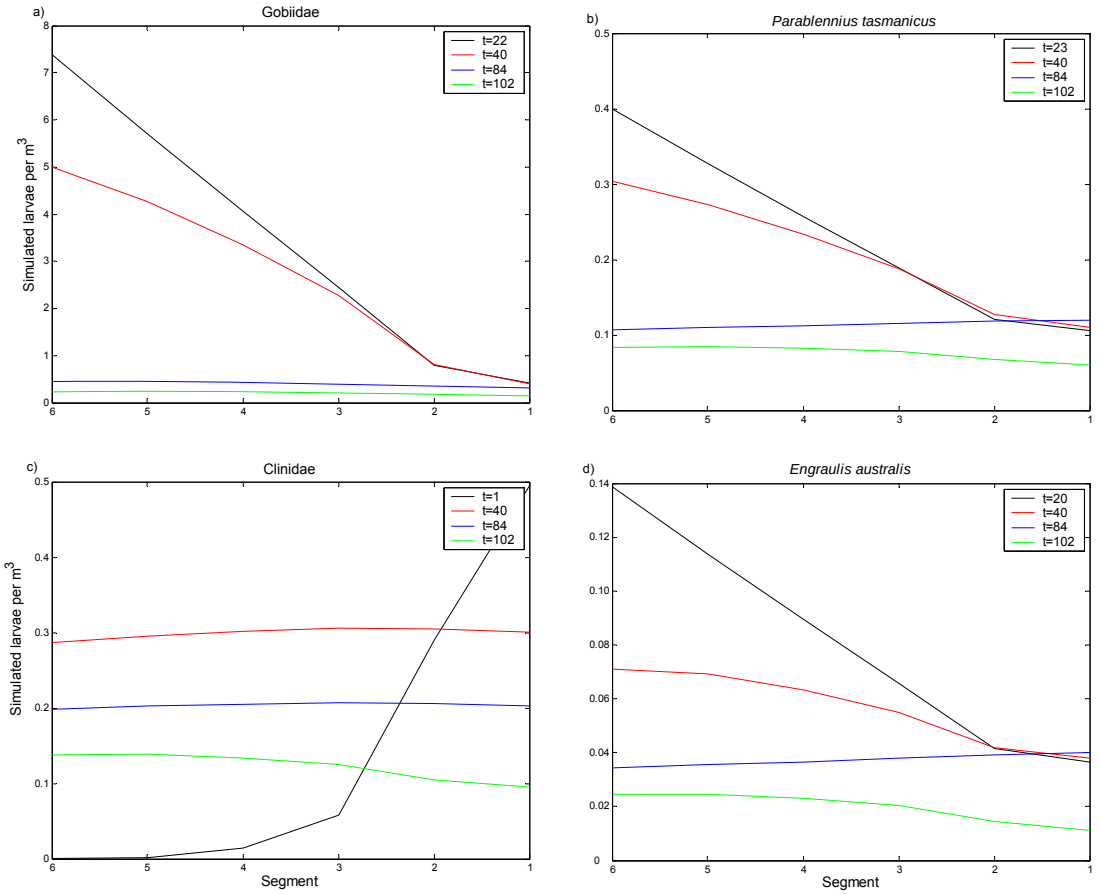

Figure 6.7. Changes in simulated concentrations of "passive" larvae of a) Gobiidae, b) *Parablennius tasmanicus*, c) Clinidae, and d) *Engraulis australis*, showing the day when maximum concentrations were attained (black), and days when the 24-hour sampling sessions were carried out (t = 40, t = 84 and t = 102).

Simulated larval concentrations of gobiids, blenniids, clinids and anchovy declined by 68, 46, 61 and 51%, respectively, from the attainment of maximum simulated concentrations to the day when the first 24-hour session took place (t = 40) (Fig. 6.7).

By the time the last sampling session was carried out (t = 102), simulated larval concentrations of gobiids, blenniids, clinids and anchovy were reduced to 3, 21, 19 and 18%, respectively.

6.4.2 Comparisons between simulated and field-obtained larval concentrations

In general, the model explained ~94% of the variability in concentrations of all larval fishes in the lower estuary, with simulated and field-obtained concentrations differing by 24% (Table 6.1). The model was accurate in predicting larval fish concentrations during December 2001 and January 2002 and in segments 2 and 6, explaining ≥78% of the variance (Table 6.1). However predictions from February 2002 and for segment 3 were not accurate enough, explaining <70% of the variance in concentration.

In December 2001, simulated concentrations of "passive" larvae followed closely the pattern of that from field-obtained concentrations, both decreasing from ~6 larvae/m^3 in segment 6 to ~1 larvae/m^3 in segment 2, with the model explaining ~98% of the variability in larval fish concentrations (Table 6.1, Fig. 6.8). The maximum difference between simulated and field-obtained concentrations in December 2001 was in segment 3 (0.87 larvae/m^3). In January 2002, the pattern of simulated and field-obtained concentrations of larval fishes were very similar, with the model explaining ~79% of the variability in larval fish concentrations (Table 6.1). The maximum difference between both simulated and field-obtained concentrations in January 2002 was in segment 6 (~0.5 larvae/m^3) (Fig. 6.8). In February 2002, the pattern followed by simulated concentrations differed from that of field-obtained concentrations with the model explaining only 49% of the variability in larval fish concentrations (Table

6.1, Fig. 6.8). The maximum difference between simulated and field-obtained concentrations in February 2002 was in segment 3 (1.2 larvae/m^3) (Fig. 6.8).

Table 6.1. Estimated variance ratio (**VR**), explained variance (**VE**) and standard deviation (**SD**) to evaluate the relationship between simulated and field-obtained concentrations of all larvae combined and those of the four dominant families.

	All larvae	**Gobiidae**	***P. tasmanicus***	**Clinidae**	***E. australis***
Overall model	**n=9**				
VR (%)	5.69	13.09	3.22	27.44	2.98
VE (%)	94.31	86.91	96.78	72.56	97.02
SD	0.24	0.36	0.18	0.52	0.17
December 2001	**n=3**				
VR (%)	2.11	9.87	2.25	23.72	0.20
VE (%)	97.89	90.13	97.75	76.28	99.80
SD	0.15	0.31	0.15	0.49	0.05
January 2002	**n=3**				
VR (%)	21.22	76.10	5.30	40.92	3.44
VE (%)	78.78	23.90	94.70	59.08	96.56
SD	0.46	0.87	0.23	0.64	0.19
February 2002	**n=3**				
VR (%)	48.72	66.01	4.58	122.54	63.21
VE (%)	51.28	33.99	95.42	-22.54	36.79
SD	0.70	0.81	0.21	1.11	0.80
Segment 2	**n=3**				
VR (%)	1.92	49.85	0.64	1.24	2.99
VE (%)	98.08	50.15	99.36	98.76	97.01
SD	0.14	0.71	0.08	0.11	0.17
Segment 3	**n=3**				
VR (%)	30.74	177.43	7.59	29.59	4.74
VE (%)	69.26	-77.43	92.41	70.41	95.26
SD	0.55	1.33	0.28	0.54	0.22
Segment 6	**n=3**				
VR (%)	0.99	0.73	2.40	76.43	1.45
VE (%)	99.01	99.27	97.60	23.57	98.55
SD	0.10	0.09	0.15	0.87	0.12

Overall, the model explained >85% of the variability in concentrations of larval gobiids, blenniids and anchovy, with simulated and field-obtained concentrations differing by <37% (Table 6.1). By contrast, only 73% of the variability of larval clinid concentrations was explained by the model, with simulated and field-obtained concentrations differing by as much as 52% (Table 6.1).

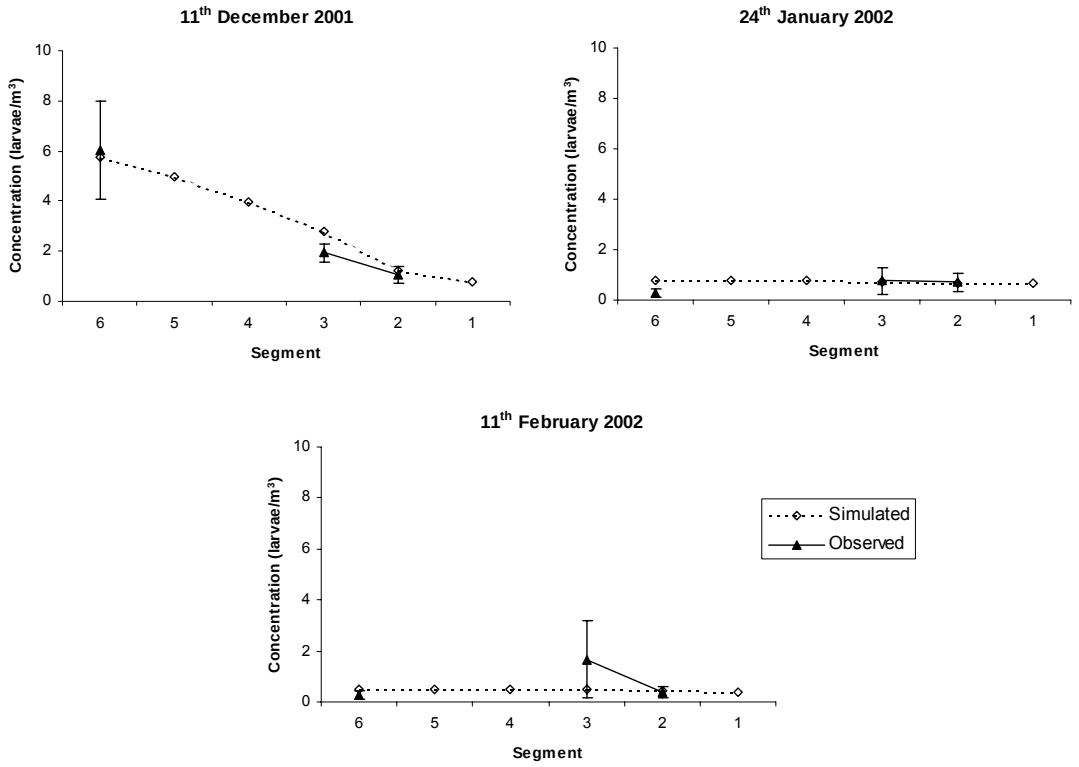

Figure 6.8. Comparison between field-obtained (±95%C.I., —) and simulated (--) concentrations of all larval fishes combined in December 2001, January 2002 and February 2002 in each of the six segments along the lower Tamar Estuary during each of the 24-hour sampling sessions.

The model did not accurately predict concentrations of larval gobiids in January and February 2002, and in segments 2 and 3, whereas it predicted them accurately only in December 2001 and in segment 6 (Table 6.1). In December 2001, the pattern followed by simulated larval gobiid concentrations was similar to that of field-obtained concentrations, with the model explaining ~90% of the variability in concentrations (Table 6.1; Fig. 6.9). The maximum difference between simulated and field-obtained concentrations in December 2001 was in segment 3 (~1.6 larvae/m^3) (Fig. 6.9). In January 2002, the pattern followed by simulated larval gobiid concentrations was

similar to field-obtained concentrations, although the model could only explain 24% of the variability in concentrations (Table 6.1, Fig. 6.9). The maximum difference between simulated and field obtained concentrations in January 2002 was in segment 2 (~0.4 larvae/m^3) (Fig. 6.9). In February 2002 the pattern followed by simulated larval gobiid concentrations differed from that of field-obtained concentrations with the model explaining only 34% of the variability in concentrations (Table 6.1, Fig. 6.9). The maximum difference between simulated and field-obtained concentrations was in segment 3 (0.9 larvae/m^3).

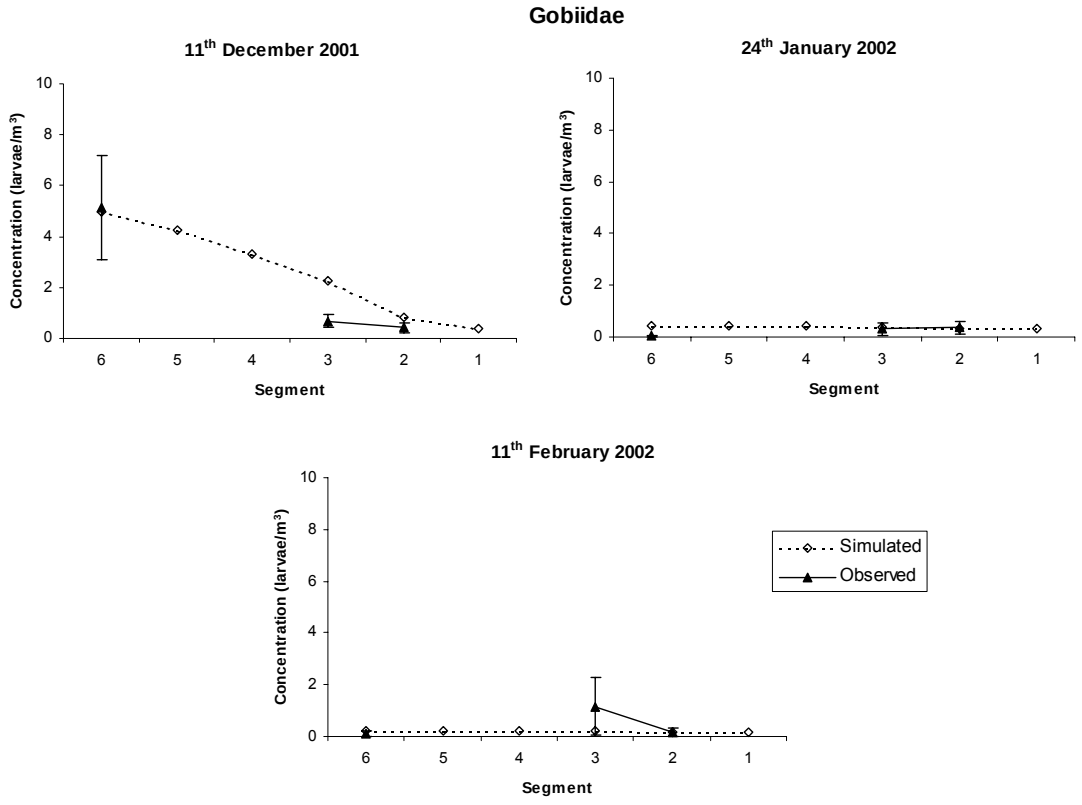

Figure 6.9. Comparison between field-obtained (±95%C.I., ─) and simulated (--) concentrations of larval gobiids in December 2001, January 2002 and February 2002 in each of the six segments along the lower Tamar Estuary during each of the 24-hour sampling sessions.

Simulated concentrations of larval blenniids were predicted accurately in all three months and segments with the model explaining >90% of the variability in concentrations (Table 6.1). In December 2001 the pattern followed by simulated larval blenniid concentrations was very similar to that of field-obtained concentrations, with the model explaining ~98% of the variability in concentrations (Table 6.1, Fig. 6.10). The maximum difference between simulated and field-obtained concentrations in December 2001 was in segment 3 (~.05 larvae/m^3) (Fig. 6.10).

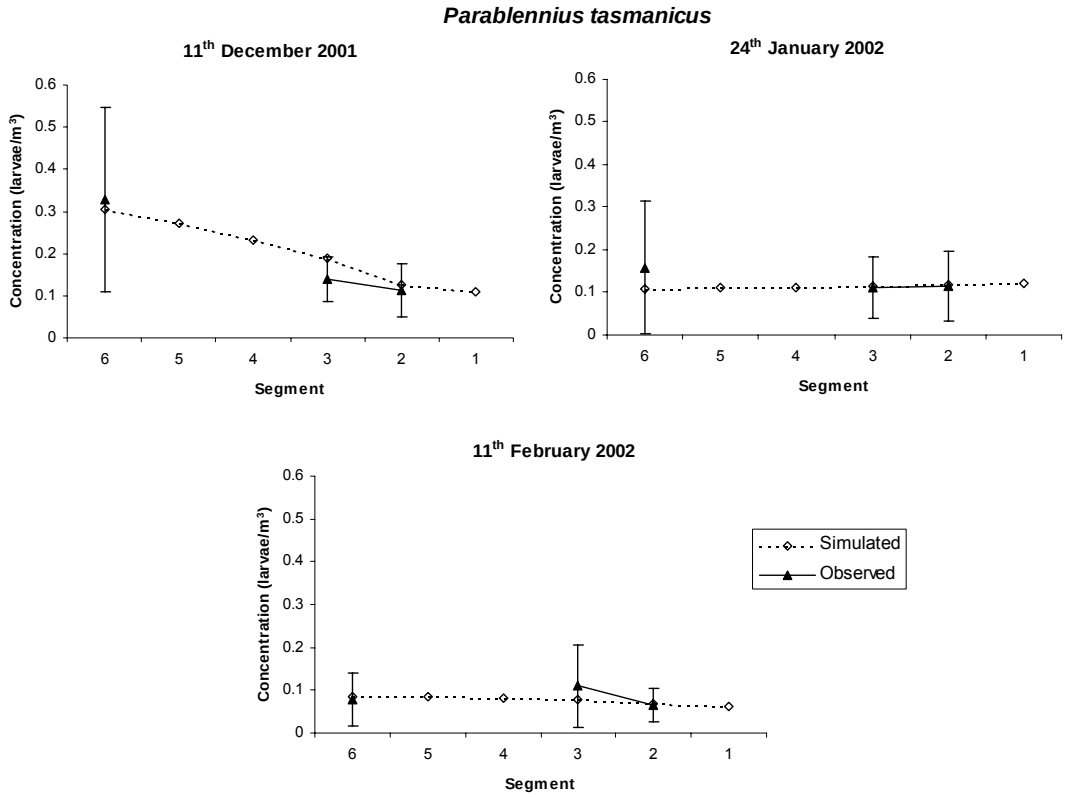

Figure 6.10. Comparison between field-obtained (±95%C.I., ⊣) and simulated (--) concentrations of larval blenniids (*P. tasmanicus*) in December 2001, January 2002 and February 2002 in each of the six segments along the lower Tamar Estuary during each of the 24-hour sampling sessions.

In January 2002, the pattern followed by simulated larval blenniid concentrations was also very similar to field-obtained concentrations with the model explaining ~95% of the variability in concentrations (Table 6.1; Fig. 6.10). The maximum difference between simulated and field obtained concentrations in January 2002 was in segment 6 (~0.05 larvae/m^3) (Fig. 6.10). In February 2002 the pattern followed by simulated larval blenniid concentrations was close to that of field-obtained concentrations with the model explaining 95% of the variability in concentrations (Table 6.1; Fig. 6.10). The maximum difference between simulated and field-obtained concentrations was in segment 3 (~0.03 larvae/m^3).

Concentrations of larval clinids were not predicted accurately in January and February 2002, and in segment 6, with the model explaining less than 60% of the variability in concentrations or adding variability to the data (Table 6.1). In December 2001, the pattern followed by simulated larval clinid concentrations was different to that of field-obtained concentrations with the model explaining only ~76% of the variability in concentrations (Table 6.1; Fig. 6.11). The maximum difference between simulated and field-obtained concentrations in December 2001 was in segment 3 (~0.4 larvae/m^3) (Fig. 6.11). In January 2002, the pattern followed by simulated larval clinid concentrations was close to that of field-obtained concentrations, with the model explaining ~59% of the variability in concentrations (Table 6.1; Fig. 6.11). The maximum difference between simulated and field obtained concentrations in January 2002 was in segment 6 (~0.2 larvae/m^3) (Fig. 6.11). In February 2002 the pattern followed by simulated larval clinid concentrations was close to that of field-obtained concentrations, although the model did not explain any of the variability in concentrations adding variability to the data (Table 6.1, Fig. 6.11). The maximum

difference between simulated and field-obtained concentrations was in segment 6 (~0.1 larvae/m^3).

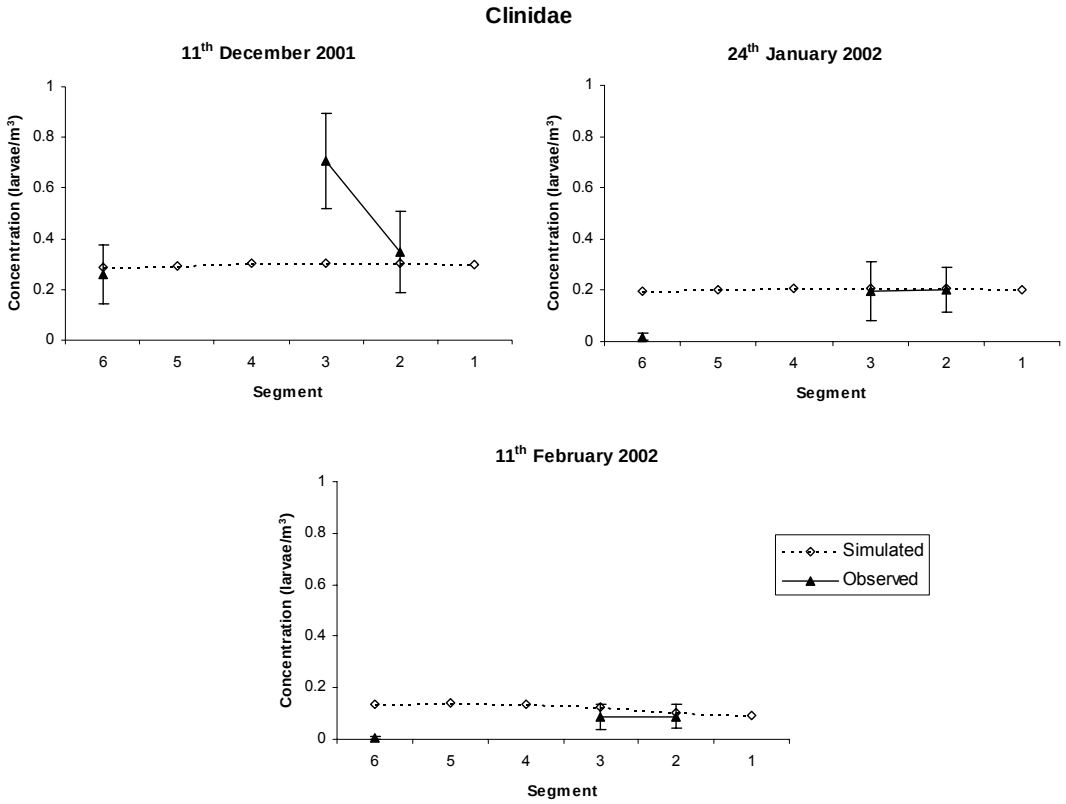

Figure 6.11. Comparison between field-obtained (±95%C.I., ─) and simulated (--) concentrations of larval clinids in December 2001, January 2002 and February 2002 in each of the six segments along the lower Tamar Estuary during each of the 24-hour sampling sessions.

Simulated concentrations of larval anchovy were accurately predicted during December 2001 and January 2002, and at all segments with the model explaining >95% of the variability in concentrations (Table 6.1). In December 2001, the pattern followed by simulated larval anchovy concentrations was very similar to that of field-obtained concentrations, with the model explaining ~99% of the variability in concentrations (Table 6.1; Fig. 6.12). The maximum difference between simulated

and field-obtained concentrations in December 2001 was in segment 2 (~.004 larvae/m^3) (Fig. 6.12).

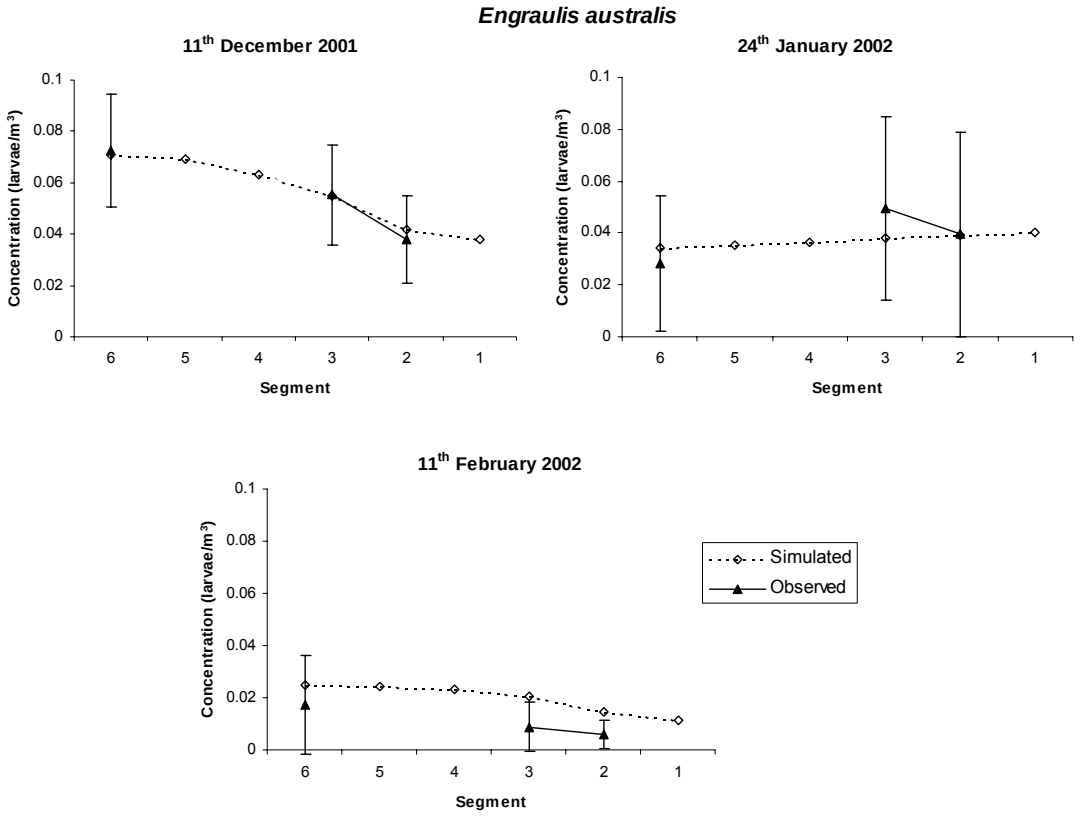

Figure 6.12. Comparison between field-obtained (±95%C.I., ⊣) and simulated (--) concentrations of larval anchovy (*E. australis*) in December 2001, January 2002 and February 2002 in each of the six segments along the lower Tamar Estuary during each of the 24-hour sampling sessions.

In January 2002 the pattern followed by simulated larval anchovy concentrations was also very similar to field-obtained concentrations with the model explaining ~96% of the variability in concentrations (Table 6.1, Fig. 6.12). The maximum difference between simulated and field obtained concentrations in January 2002 was in segment 3 (~0.01 larvae/m^3) (Fig. 6.12). In February 2002, the pattern followed by simulated larval anchovy concentrations was close to that of field-obtained concentrations with

the model explaining only 37% of the variability in concentrations (Table 6.1, Fig. 6.12). The maximum difference between simulated and field-obtained concentrations was in segment 3 (~0.01 larvae/m^3).

6.5 Discussion

Overall, there was a close correspondence between simulated and larval fish concentrations obtained along the lower Tamar Estuary between December 2001 and February 2002. However, this agreement was mainly due to the accuracy of the model in predicting concentrations in segments 2 and 6, which was achieved by setting the boundary conditions in Bass Strait following field-obtained larval fish concentrations in segment 2 and by choosing suitable loads for segment 6 in order to match simulated and field-obtained concentrations as much as possible. Results yielded by the application of this 1-dimensional transport model, which assumed that larvae behaved as passive particles is just the first step to identify the mechanisms involved in larval fish dynamics in a highly flushed environment. The "passive" particle assumption relies on information that larvae at an early stage behave in a similar way to passive contaminants and, as such, are distributed by the same processes that distribute salt and temperature, i.e. advection and diffusion (Fortier and Leggett, 1982; de Lafontaine *et al.*, 1984; Jenkins and Black, 1994; Brown *et al.*, 2004; Mao *et al.*, 2004).

The fact that the selected loads in segment 6 yielded a close correspondence between simulated and field-obtained concentrations (>95%) indicates that the representation

of the larval fish production rate and its decline in time reasonably estimated the main spawning peak and spawning duration in the Tamar Estuary. The sharp decline in field-obtained larval fish concentrations towards February 2002 could be reflecting both the duration and completion of the spawning activity in the area, as well as mortality through loss via the net seaward currents (Jacquaz *et al.*, 1977; Fortier and Leggett, 1982).

Differences between simulated and field-obtained larval fish concentrations became more apparent as time progressed. While the model could explain ~98% of the variability in concentrations in December 2001, only 79 and 51% of the variability in concentrations was explained in January and February 2002, respectively. Ontogenetic changes in the behaviour as well as increased swimming ability of larvae, could be a plausible explanation to the increasing discrepancy between simulated and field-obtained concentrations in January and February 2002. Visual inspection of samples showed a general increase in postflexion stage larvae in January and February 2002. Since the ability to undertake vertical migrations improves as larvae develop, the presence of postflexion larvae capable of migrating vertically and potentially reduce their horizontal drifting by 30% will therefore explain the lack of correspondence between simulated and field-obtained concentrations in these months, as larvae behaved differently to passive particles (Fortier and Leggett, 1982; Hill, 1991; Tzeng and Wang, 1993; Harris *et al.*, 1999).

In the case of segment 3, the simulated concentrations were inaccurate in most months possibly because the model was not forced to match field obtained concentrations in this segment, unlike segments 2 and 6 where the boundary conditions and load input

were set in order to match simulated and field-obtained concentrations. In addition, the model used in this study is 1-dimensional and factors such as velocity and concentrations correspond to a spatial average over a cross section for a specified period of time, hence lateral gradients of larval concentrations and velocities are not considered (Ward and Espey, 1971). This, will mask the complex hydrodynamics occurring in segment 3, such as the secondary flow going in the opposite direction of the main current at the eastern side of the estuary (see Chapter 2 for details). Consequently, this type of model may not be well suited to explain the variation in the concentrations in areas subjected to strong lateral velocity gradients such as the conditions found in segment 3.

All simulations carried out for larval gobiids, blenniids and anchovy started with an input of particles to the model in segment 6, given the high concentrations of larvae of those groups obtained in that segment during December 2001. The distribution of larvae of those groups in December 2001, as well as the fact that most were preflexion, suggests they may have been spawned upstream of segment 6. Since the extent of the transport of early stage larvae depends mainly on the flushing time of the estuary and spawning location (Fortier and Leggett, 1982), this spawning location is very important to determine survival and year class strength of estuarine species in the Tamar Estuary.

In the case of gobiids, the reasons provided for the discrepancies between simulated and observed gobiid concentrations could be the same as those for all larval fishes: larval mortality at early stages through loss due to net seaward flow, complex hydrodynamics in the area and behavioural changes such as vertical migration by

postflexion larvae (DeWolf, 1973; Fortier and Leggett, 1982; Norcross and Shaw, 1984; Hill, 1991; Tzeng and Wang, 1993; Harris *et al.*, 1999; Brown *et al.*, 2004). However, there were more discrepancies between simulated and field-obtained larval gobiid concentrations than between the simulated and field-obtained overall larval fish concentrations. This could be due to adaptations of adult gobiids to estuarine environments such as repeat spawning, demersal eggs, some level of parental care and rapid settling (Leis and Rennis, 1983; Miller, 1984; Beckley, 1985; Neira *et al.*, 1992), helping their larvae to remain within the Tamar Estuary and hence affecting the model predictions, which did not consider these factors.

The discrepancy between simulated and field-obtained larval anchovy (*E. australis*) concentrations in February 2002 could probably be due to ontogenetic changes in their behaviour, that is the increasing use of vertical migrations by older larvae (late postflexion) to reduce drifting (Fortier and Leggett, 1982; de Lafontaine *et al.*, 1984; Tzeng and Wang, 1993; Jenkins and Black, 1994; Harris *et al.*, 1999; Brown *et al.*, 2004; Mao *et al.*, 2004). Since the flushing time estimated for the lower estuary during summer is ~25 days, and the estimated age of postflexion anchovy is ~13 to 24 days (Raudzens, 2006), their distribution upstream of segment 6 would provide enough time for larval anchovy to reach the postflexion stage before being flushed out of the system. This upstream distribution could be important since unlike gobiids and blenniids, larval anchovy hatch from pelagic eggs and newly hatch larvae are less develop than those from gobiids and blenniids. Moreover, this will enable early preflexion stage anchovy to remain within a food-rich environment during the time when their swimming capabilities are very poor (Newton, 1996).

The fact that the model could explain larval blenniid (*P. tasmanicus*) concentrations in all segments and months could be probably due to blenniid larvae behaving similar to passive particles. This is supported by the fact that no apparent change was observed in the stage of larval blenniids and larvae from this family are known to use ebb currents to exit estuaries before returning at a metamorphic or post-larval stage (Beckley, 1985, 1986; Roper, 1986; Whitfield, 1989a,b). This behaviour suggests that blenniids in the lower Tamar Estuary may be advected out of the system continuously at an early stage, i.e. preflexion, and may be the main reason for the close correspondence between simulated and observed blenniid concentrations.

In the case of clinids, the model was only able to explain 72% of the variability, with the model explaining with some accuracy the variability in concentrations only in December 2001 and in segments 2 and 3. Since clinid concentrations were usually higher downstream than upstream, values for the boundary conditions were set to correspond to the concentrations obtained in segment 2, and hence why the model predictions worked better for that segment. The fact that clinids are live bearers implies that larval clinid were in the same areas as adults and this, may have influenced the model simulations since the close proximity between the source of larvae and the settlement sites could potentially cause low performance in model simulations (Brown *et al.*, 2005).

The advantage of 1-dimensional transport models is that the utilization and prediction of information is related to accessible observational data (Ward and Espey, 1971). Results of this study suggest that the use of this particular model should only be indicative, since it simplifies the hydrodynamics of the estuary and its accuracy will

mainly rely in the ability to force the model to match field-obtained concentrations, like in the case of segments 2 and 6. However, this model was sufficient to provide a general overview on how the circulation influenced the distribution of larval fishes and, more importantly, it provided a base to understand the spawning activities in the Tamar Estuary. The consideration of vertical and lateral differences in advection and diffusion, increasing field-field obtained data for ground truthing, as well as the estimation of larval mortality (sinks) and vertical migrations in future models, should allow a better understanding of the role played by physical forces compared to the biological components (e.g. active swimming, vertical migration, spawning strategies and location) in the distribution of larval fishes.

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Chapter 7

General discussion

7.1 Overview

This thesis presents the results of the first, most extensive field-study of larval fishes and zooplankton, including environmental and physical data, ever to be undertaken in the Tamar Estuary, in northern Tasmania. It is expected that the data collected during this study be used as a baseline for future studies in ecology and ecosystem management in the estuary, given that it is regarded as one of the most degraded estuaries in Tasmania, having severe siltation and the largest rice grass infestation in all Australia (Edgar *et al.*, 1999).

The study was designed to test the hypothesis that the dynamics of larval fishes in a highly flushed estuary such as the Tamar differs from the behaviour exhibited by larval fishes in estuaries subjected to weaker tidal currents. To approach this problem, it was necessary to examine a number of significant biotic and abiotic factors, and ways in which these may influence the spatial and temporal distribution of larval fishes in the estuary (Fig. 7.1). These factors included water temperature, freshwater flows, tidal currents, salinity, water circulation and zooplankton biomass, all of which combined, influence changes in family composition, abundance and spatial distribution of larval fishes in the Tamar Estuary, as well as transport and retention of certain taxa.

Since abiotic factors generally have a stronger impact on many fish species than biotic factors (Baltz *et al.*, 1998; Meng and Matern, 2001; Peterson *et al.*, 2004), it is necessary firstly to describe the hydrographic characteristics of the Tamar Estuary before discussing the overall link between environmental variables, secondary production and larval fish dynamics.

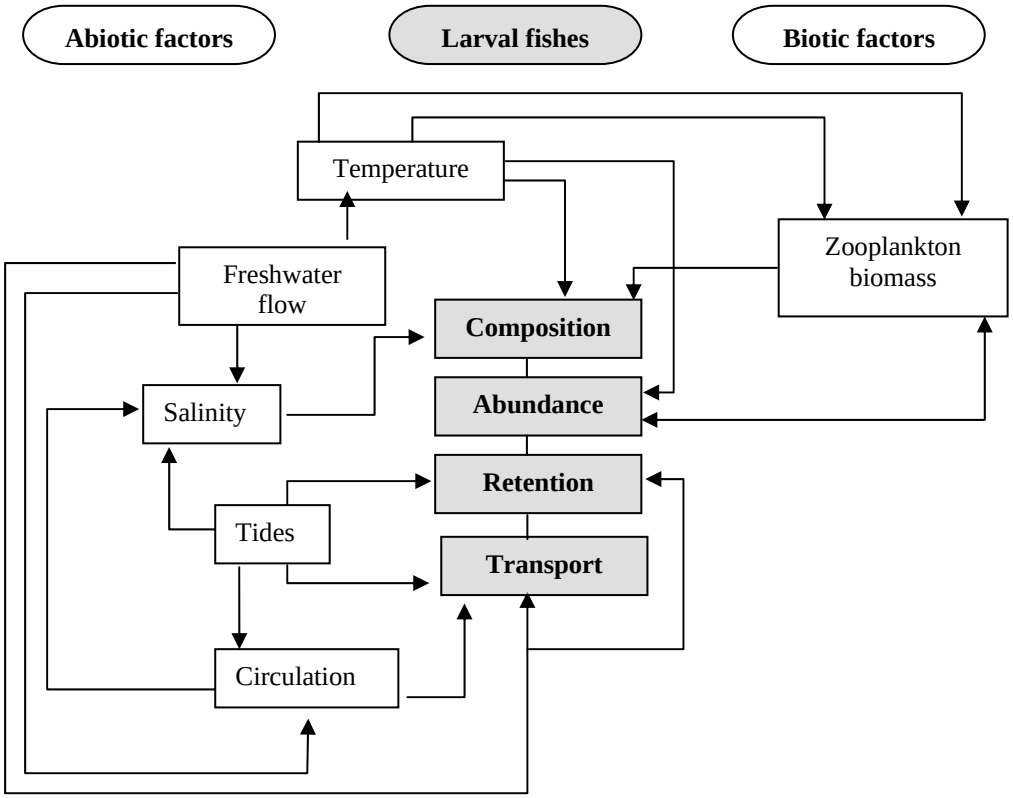

Figure 7.1. Flow diagram showing the links of the array of biotic and abiotic factors examined in this study in relation to the larval fish dynamics.

7.2 The physical environment

The Tamar Estuary extends approximately 70 km from Bass Strait to the city of Launceston and follows a winding course comprising a series of shallow, extensive bays interconnected by channels as narrow as 300 m, and an uneven bathymetry of 2-

50 m. Data of salinity, current velocities and freshwater flow obtained during this study led the Tamar to be classified as Type 2a, or partially mixed estuary (Hansen and Rattray, 1966). However, it was also found that during peak flood season, the upper reaches change from an almost well mixed to a salt wedge, or Type 4, estuary. The upstream salt flux in the Tamar is mainly by diffusion (i.e. tidal mixing), with gravitational convection playing only a small role. The vertical stratification of temperature and salinity is weak, except in the upper reaches during peak flood season, and current velocities are considerably strong (± 2 m/s), suggesting the absence of a two-layered circulation pattern, a key feature to understand various physical, chemical and biological processes.

Mean freshwater flow from the North and South Esk rivers during the study period was higher during spring (140 m^3/s) and lower during winter (47 m^3/s), with the South Esk supplying most of the freshwater runoff. Tides are semidiurnal, with a moderate diurnal inequality and a tidal range of 3 m at Georgetown and 3.5 m at Launceston (Phillips, 1975; Pringle, 1982; Bell, 1996). The tidal cycle comprises an approximately 6-hour flood and 7-hour ebb tide, with flood currents being 0.2-0.4 m/s stronger than ebb currents, which makes the Tamar Estuary a flood-dominated system. The estimated exponential flushing time along the lower Tamar Estuary during moderate freshwater runoff (75 m^3/s) is ~10 days, while a simulated 90% reduction in tracer concentrations would take ~25 days. All these characteristics, i.e. weak vertical stratification, strong tidal mixing and lack of two-layered circulation, make the Tamar a unique estuary in Tasmania. This uniqueness parallels the classification made by Edgar *et al.* (1999) who distinguished the Tamar from all other Tasmanian estuaries as the only mesotidal drowned river valley.

7.3 Cycles in zooplankton biomass and larval fish abundance

This study investigated the relationship between zooplankton biomass and larval fish abundances, with the former regarded as a proxy for secondary production in the Tamar Estuary. Peaks in zooplankton biomass occurred in November, both in 2001 and November 2002, when temperatures were ~15°C. This spring peak, some two months before the attainment of maximum temperatures (~19°C), parallels that in other temperate estuaries worldwide (Table 7.1). Larval fish concentrations also peaked in November both in 2001 and 2002, similar also to the situation with other temperate estuaries, where peak larval fish concentrations occurred 2-4 months before peaks in temperatures (Table 7.1).

Table 7.1. Estuaries (E) and enclosed bays (EB) where concentrations of zooplankton biomass (ZB) or larval fishes (LF) peaked during late-spring/early-summer, i.e. 2-4 months before the annual peak in water temperature.

System	E/EB	LF/ZB	References
Long Island Sound (United States)	E	ZB	(Capriulo *et al.*, 2002)
Chesapeake Bay (United States)	E	ZB	(Roman *et al.*, 2005)
Seine (France)	E	ZB	(Mouny and Dauvin, 2002)
Gironde (France)	E	ZB	(Sautour and Castel, 1995)
Ems (Netherlands)	E	ZB	(Sautour and Castel, 1995)
Westerchelde (Netherlands)	E	ZB	(Sautour and Castel, 1995)
Swan Estuary (Australia)	E	LF	(Neira *et al.*, 1992)
Botany Bay (Australia)	EB	LF	(Steffe and Pease, 1988)
Algoa Bay (South Africa)	EB	LF	(Beckley, 1986)
Whangateau Harbour (New Zealand)	EB	LF	(Roper, 1986)

The match between peaks in zooplankton biomass and larval fish concentrations in the Tamar Estuary contrasts with the mismatch described for the Hopkins River in Australia and Newport River in United States, where zooplankton peaked 1-2 months before larval fish concentrations (Thayer *et al.*, 1974; Newton, 1996). This suggests

that the timing in the larval fish occurrence in the Tamar is strongly related to both increasing temperature and zooplankton production cycles, both of which are key factors in triggering reproductive activities of temperate fishes (Bye, 1984; de Lafontaine *et al.*, 1984).

No evident difference in the spatial distribution both of zooplankton biomass and larval fish concentrations was found in the Tamar Estuary, following examination of these data using the Venice system of salinity regions. In the case of zooplankton biomass, this lack of evident spatial pattern contrasts the findings in temperate estuaries such as the Seine, Gironde, Ems and Westerschelde, where the greatest biomasses were recorded in the mesohaline or oligohaline region (Sautour and Castel, 1995; Mouny and Dauvin, 2002). Likewise, the lack of a spatial pattern in larval fish concentrations between salinity regions contrasts that found in several South African estuaries, where the greatest concentrations were obtained in the mesohaline (5-17.9 PSU) region (Strydom *et al.*, 2003). A number of factors could affect the distribution of zooplankton biomass and larval fish concentrations in the Tamar Estuary leading to a lack of spatial pattern, including the strong tidal currents (~2 m/s) which may be responsible for redistributing concentrations more uniformly along the estuary. While spatial differences in larval fish concentrations have also been reported in other temperate estuaries worldwide, none of these studies used the Venice system thus making it difficult to draw comparisons with this study.

The consistent timing in the annual peak in larval fish concentrations recorded in the Tamar Estuary implies a regularity in the spawning time. This in turn suggests that a number of fish species in the Tamar may have fixed spawning periods to ensure a

match between larvae and food supply (Cushing, 1975; Bye, 1984). Spawning regularity has also been reported for other temperate estuaries, where peaks in larval fish abundance occurred during the same month across different years (de Lafontaine *et al.*, 1984; Drake and Arias, 1991; Witting *et al.*, 1999).

Considering the occurrence of larvae, the main spawning season of some estuarine fish groups in the Tamar (e.g. gobiids, blenniids and anchovy), appeared to last ~2 months, as indicated by the fact that the peak in larval fish concentrations lasted only two months (November to December) before decreasing rapidly. This rather short spawning season was clearly predicted in the 1-dimensional transport model as an exponential decline with an decaying time of ~5 days (see Chapter 6). The close correspondence between the simulated and field-obtained larval fish concentrations suggests that the model representation of a short but intense spawning season was reasonable in the case of these fish groups. The comparatively short spawning season in the Tamar Estuary differed from that reported in other Australian temperate estuaries where larvae have been caught over a protracted period of time, i.e. 4 months, such as the Hopkins River, Swan Estuary, Nornalup-Walpole Estuary and Wilson Inlet (Gaughan *et al.*, 1990; Neira *et al.*, 1992; Neira and Potter, 1992b, 1994; Newton, 1996).

Another aspect of the Tamar Estuary that may be relevant to larval fishes is the presence of big swarms of large jellyfishes during March and April 2002, at the time when concentrations of larval fishes and zooplankton biomass were very low. Although it is not known whether these jellyfishes represent one or more species, significant predation by jellyfish on larval fishes and other zooplankters has been

reported in several temperate estuaries worldwide (Fancett and Jenkins, 1988; Newton, 1996; Esteves *et al.*, 2000; Capriulo *et al.*, 2002; Roman *et al.*, 2005). The presence of these jellyfishes at the time of low larval fish abundances suggests that the spawning timing and duration of fishes in the Tamar Estuary may be influenced to some extent by predator presence. This observation is supported by the fact that both eggs and yolk-sac stage larvae are more vulnerable than postlarval stages as they are unable to avoid predatory jellyfishes (Fancett and Jenkins, 1988; Esteves *et al.*, 2000). In addition, it has also been suggested that the historical impact of predation in some fish species may have modified the reproductive behaviour of adults in order to reduce larval loss due to predation (Frank *et al.*, 1982; Esteves *et al.*, 2000). In the case of the Tamar, however, it is still unknown whether larval survival depends on density-independent (e.g. temperature and advection) or density-dependent (e.g. starvation and predation) mechanisms, or both (Bailey and Houde, 1989; Houde, 1997; Esteves *et al.*, 2000). In any case, it is possible that both the start of the spawning season as well as the intensity of spawning in the Tamar are related to abiotic factors, such as increasing temperature and moderate freshwater flow, whereas spawning duration may be linked to biotic factors, such as presence of potential predators and food availability.

7.4 Larval fish assemblages

Results of this study indicate that the taxa composition of larval fish assemblages in the Tamar Estuary was strongly influenced by temperature and zooplankton biomass. Whereas there are no comparable data on larval fish assemblages from other estuaries in Tasmania, the dominance of larval gobiids, blenniids, clinids and anchovy parallels

that reported for other estuaries and enclosed bays in temperate Australia and South Africa, where assemblages are characterized by high abundances of a few taxa and gobiids are always the most dominant family (Gaughan *et al.*, 1990; Potter *et al.*, 1990; Neira *et al.*, 1992; Neira and Potter, 1994; Whitfield, 1999; Neira and Sporcic, 2002; Strydom *et al.*, 2003). In addition, the number of families represented as larvae in the Tamar (44) was comparatively higher than that of other temperate estuaries and enclosed bays in Australia and elsewhere, although in some systems this could be a result of sampling intensity (Table 7.2).

Table 7.2. Number of families and sampling duration of larval fish studies carried out in selected estuaries (E) and enclosed bays (EB) in Australia and worldwide.

System	E/EB	Number of families	Sampling duration	References
Tamar Estuary (Australia)	E	44	14 months	This study
Great Bay-Little Harbour (United States)	E	43	6 years	(Witting *et al.*, 1999)
Lake Macquarie (Australia)	E	41	2 tidal cycles	(Trnski, 2001)
Swan Estuary (Australia)	E	37	1 year	(Neira *et al.*, 1992)
Port Phillip Bay (Australia)	EB	32	1 year	(Neira and Sporcic, 2002)
Algoa Bay (South Africa)	EB	26	2 years	(Beckley, 1985)
Narragansett Bay (United States)	E	25	1 year	(Keller *et al.*, 1999)
Nornalup-Walpole (Australia)	E	23	1 year	(Neira and Potter, 1994)
Whangateau Harbour (New Zealand)	EB	23	1 year	(Roper, 1986)
Cadiz Bay (Spain)	EB	21	5 years	(Drake and Arias, 1991)
Wilson Inlet (Australia)	E	17	19 months	(Neira and Potter, 1992b)
Swartkops (South Africa)	E	15	2 years	(Melville-Smith and Baird, 1980)
Permanently open estuaries in East Cape coast (South Africa)	E	23	1 year	(Strydom *et al.*, 2003)
Hopkins River (Australia)	E	9	20 months	(Newton, 1996)
Taieri/Waipori (New Zealand)	E	7	5 months	(Sutherland and Closs, 2001)

Of the 44 families identified during this study, larvae belonging to 28 families were more abundant throughout the lower estuary or were caught exclusively at sites near the entrance, and occurred mostly during late spring/early summer. These included the few marine-spawned larvae of families such as Bothidae, Gerreidae,

Hemiramphidae, Ophidiidae, Sillaginidae, Pegasidae and Scombridae, which have also been caught in the adjacent marine area around the entrance of the estuary during the same season (Raudzens, 2006). The presence of these marine-spawned larvae indicates that the lower estuary, as far in as Georgetown (see Fig. 2.1 for reference), could be considered as an extension of Bass Strait, and that most may incidentally be flushed into the estuary (Beckley, 1985; Roper, 1986; Steffe and Pease, 1988; Drake and Arias, 1991; Neira *et al.*, 1992; Neira and Potter, 1994; Keller *et al.*, 1999).

There was a clear pattern in the spatial distribution of the larval fish assemblages in the Tamar Estuary during the peak concentration period, with one assemblage occurring from the entrance to 35 km upstream and another one occurring in the middle region >35 km upstream. The first assemblage was characterized mainly by estuarine-dependent larvae, such as gobiids, blenniids, anchovy and clinids, while the second assemblage was characterized by larvae of freshwater taxa such as those of galaxiids. However, there was no clear definition of assemblages found close to the entrance, which contained the highest number of families. The distinction between the two assemblages was found to be mainly driven by salinity and, to a lesser extent, by freshwater flow, which limited the spatial distribution of the larvae of at least the less tolerant families such as Clinidae (25-35 PSU). In addition, neither assemblage in the Tamar showed the clear distribution pattern typical of temperate estuaries, which normally follows a pattern closely associated to the Venice salinity system (Strydom *et al.*, 2003) or to estuary regions (Neira *et al.*, 1992; Neira and Potter, 1994).

It is likely that a reason for the geographical extent of each larval assemblage in the Tamar Estuary may be associated with the strong diffusive forces of the tidal currents,

which could take larvae to areas far from where they originated, including those that are competent swimmers (Fortier and Leggett, 1982). This in turn suggests that the distribution of larval fishes in a preferred salinity range is directly affected by currents and circulation patterns within the system, and that larvae would have to employ mechanisms to either remain in or reach a preferred zone in the estuary (Weinstein *et al.*, 1980).

7.5 Transport and retention

Larval fish concentrations in the lower Tamar Estuary differed primarily with diel cycles and secondarily with tidal cycles. This is likely due to the estuary being a highly-flushed system without a two-layered circulation, and where the use of selective tidal transport by larval fishes to enter/exit is not as important as is in two-layered systems such as Cape Fear River Estuary (Weinstein *et al.*, 1980). Instead, the pattern described for the Tamar Estuary parallels that described for other estuaries or sections of estuaries with strong tidal currents >1.5 m/s, and weak vertical stratification, and where diel cycles have been shown to be more important than tidal cycles (Roper, 1986; Whitfield, 1989a; Churchill *et al.*, 1999; Forward Jr *et al.*, 1999; Trnski, 2001).

The lack of evident tidal patterns exhibited by larval fishes in December 2001 and January 2002 may be due to larvae being mainly at a preflexion stage, i.e. when larvae are unable to undertake vertical migrations or employ other type of behaviour to remain within the estuary (Fortier and Leggett, 1982; de Lafontaine *et al.*, 1984; Tzeng and Wang, 1993; Jenkins and Black, 1994; Harris *et al.*, 1999; Brown *et al.*,

2004; Mao *et al.*, 2004). This is supported by the fact that a tidal pattern was observed during February 2002, when most larvae were caught at the postflexion stage. However, this tidal pattern displayed by larval fishes in February 2002 was always in conjunction with a diel cycle, and even though net avoidance may have played a role in the diel pattern observed, behaviours such as vertical migration may have also taken place and, as such, these may have included a tidal component.

The 1-dimensional transport model utilized during this study showed that simulated concentrations of larval fishes were similar to field-obtained concentrations, with larvae drifting downstream from December 2001 to January 2002. This displacement, which can be used as an indicator of the extent of transport within the lower estuary, suggests that larvae at the preflexion stage behaved similarly to passive particles and, according to the model, they are flushed out of the system in ~25 days. However, the estuarine transport model could not predict the concentrations of postflexion larvae, as these may be able to adjust their vertical distribution and significantly reduce their horizontal drift (Fortier and Leggett, 1982; Hill, 1991).

7.6 Strategies adopted by larval fishes in a highly-flushed estuary

Strategies employed by larval fishes to survive in estuaries are species-specific, and include selective tidal transport, remaining near or at the bottom, key spawning location and ontogenetic changes (Weinstein *et al.*, 1980; Boehlert and Mundy, 1988; Epifanio, 1988; Shaw *et al.*, 1988; Norcross, 1991; Brown *et al.*, 2005). In addition, it is likely that these strategies would differ between highly-flushed and weakly flushed estuaries. Herewith, the possible strategies displayed by each of the dominant families

recorded during this study are discussed. Although the larvae of two of these families were not identified to species level, it was deemed appropriate to point out some general strategies at the family level.

Gobiidae

Gobiids constitute one of the most abundant groups in temperate estuaries worldwide, and are probably the best adapted to survive in estuarine environments (Potts, 1984). Most gobiid species are repeat spawners, and could in some cases spawn over a protracted time period (Miller, 1984). This is typically the case of many, if not most, temperate estuaries in Australia and South Africa (Beckley, 1985; Neira *et al.*, 1992; Neira and Potter, 1992b; Newton, 1996). The set of strategies used by gobiids, e.g. high fecundities, demersal eggs, repeat spawning and parental care, will enable them to secure the recruitment of their larvae to the adult population habitats in highly-flushed systems like the Tamar Estuary where larval loss could be high due to strong currents, as in the case of estuaries such as Whangateau Harbour in New Zealand and Beaufort Inlet in United States (Roper, 1986; Churchill *et al.*, 1999; Forward Jr *et al.*, 1999). In the Tamar Estuary, gobiid larvae peaked during two months, November and December, with mean concentrations decreasing from 260 larvae/m^3 in December 2001 to 2 larvae/m^3 in January 2002. This relatively short larval occurrence period suggests that species from this family in the Tamar Estuary may not be spawning over protracted periods as in weakly flushed systems, but instead spawn intensively during a short period. Moreover, the seasonal abundance of larval gobiids in the Tamar followed the short zooplankton biomass peak, which suggests that spawning duration may be linked to food availability while spawning frequency could be driven by the increase in temperature during spring (Miller, 1984).

The proportion of gobiids obtained during the routine sampling in the middle and upper regions was almost ~8% higher than that obtained in the lower estuary during the peak concentration period, suggesting that gobiid species in the Tamar may be spawning predominantly in the middle and upper regions. Given the flushing time predicted by the model for the lower estuary (~25 days), the above implies that gobiid larvae originating upstream would have enough residence time to reach a size where they would be capable of migrating vertically, or settle onto their adult habitats. Spawning in middle regions of highly-flushed estuaries therefore, could be a key factor for the survival of their larvae and subsequent recruitment to the adult populations, since some gobiid species have the ability of settling and reaching sexual maturity very rapidly (~ 3 months) (Miller, 1984). In addition, the extent of the transport of early stage larvae depends on spawning location, as well as the flushing time of the estuary (Fortier and Leggett, 1982; Miller, 1984). Spawning of gobiids in upper estuary reaches is not exclusive to highly-flushed estuaries like the Tamar, as several species also spawn in the middle and upper regions of other temperate Australian estuaries characterized by weak tidal currents (Neira *et al.*, 1992; Neira and Potter, 1992a,b, 1994; Newton, 1996).

Ontogenetic changes in the behaviour of larval gobiids became apparent during the 24-hour sampling carried out in December 2001 – February 2002. Although larvae were not sorted into different developmental stages, visual inspection of samples showed an evident difference in the percentage of different larval stages across months. Most larvae caught during December 2001 were preflexion, whereas most caught in February 2002 were postflexion. Early stage larvae have poor swimming

ability, which combined with the strong tidal currents in the Tamar, may have resulted in larval gobiid concentrations found in segment 6 (see Chapter 6) being advected towards the mouth in ~1 month, suggesting a behaviour similar to passive particles (Roper, 1986; Forward Jr *et al.*, 1999). By contrast, the distribution of gobiid larvae changed from no pattern at all to a diel pattern in January 2002, and to a diel and tidal pattern in February 2002, suggesting a change in behaviour which may have helped these larvae to reduce their drifting and thus remain or exit the lower estuary. Changes in the distribution of gobiid larvae were also examined with the estuarine transport model, which assumed that larvae were passive particles. Model runs accurately predicted the larval concentrations during December 2001, when larvae were mostly preflexion. However, predictions were inaccurate in January and February 2002, likely because of the presence of postflexion larvae, which would have behaved differently from passive particles.

High abundances of larval gobiids being passively swept out of estuaries during ebb tides have been reported in moderately flushed estuaries in South Africa, New Zealand and Australia (Beckley, 1985, 1986; Roper, 1986; Whitfield, 1989a,b; Neira and Potter, 1992a). In highly-flushed estuaries, like the Tamar, preflexion gobiid larvae cannot avoid being flushed in or out of the estuary. Nevertheless, postflexion larval gobiids appeared also to be leaving the system on the night ebb tide in February 2002. This suggests that larvae of some gobiid species may have been spawned within the estuary and then exited the system at a later stage. On the other hand, there may also be other gobiid species that could be completing their entire life cycle within the estuary, as well as species that may have been spawned near coastal waters and enter the estuary at a late larval/early juvenile stage. It is possible that for most gobiid

species an important strategy in highly-flushed estuaries may be to spawn in key locations depending on their life cycle, and to have a short, intense spawning periods timed with abundant food production. In this context, it is worthwhile mentioning that since the Gobiidae in the Tamar Estuary may comprise at least five species, these results should only be indicative as species could use different strategies.

Parablennius tasmanianus

Larval blenniids (*P. tasmanianus*) were the second most abundant taxa in the estuary. Most were spawned in the lower estuary as shown by the fact that the proportion of larvae was 5% higher along the lower estuary compared to the middle region during the peak season. However, there is also the possibility that some larval blenniids were spawned in the coastal areas off the entrance of the Tamar Estuary as reported by Raudzens (2006).

Blenniids were the only dominant group that displayed a tidal distribution pattern, with larvae apparently being flushed out of the estuary during the ebb tide at all times. This pattern parallels that of larval blenniids in estuaries in South Africa and New Zealand, and has led to the consideration of a fourth life history category that also includes some gobiids, i.e. resident estuarine species whose preflexion larvae leave the system on ebb tide before returning as postlarvae (Beckley, 1985, 1986; Roper, 1986; Whitfield, 1989a,b; Neira and Potter, 1992a).

No apparent ontogenetic changes in the behaviour of blenniids were evident following visual examination of samples taken across summer months. The lack of ontogenetic change was supported by the fact that the transport model could accurately predict

larval blenniid concentrations in all months. Plausible explanations to the observed tidal pattern is that blenniids could be using some means to tidally synchronize their hatching, or use rheotaxis after hatching to synchronise their exit with ebb currents, as larval fishes can apparently detect current speeds of 1-10 cm/s (Arnold, 1981; Boehlert and Mundy, 1988). An advantage that could also aid larval blenniids to exit the system at an early stage is the ability to lay demersal eggs. This observation can be made from the fact that the absence of two-layered circulation in the Tamar Estuary would prevent newly-hatched larvae from being transported upstream, given that current velocity decreases near the bottom due to friction (Ippen, 1966; Leis and Rennis, 1983; Miller, 1984; Beckley, 1985; Neira *et al.*, 1992). It is highly likely that larval blenniids inside the Tamar employ both mechanisms, i.e. tidally synchronizing hatching as well as remaining near the bottom except on the ebb tides.

Clinidae

Larval clinids were the third most abundant taxa during this study. Most were caught within the entrance of the Tamar Estuary, implying they may have been either born in the vicinity of the mouth outside and advected into the estuary or born within the lower estuary. One of the reasons clinids give birth very close to the entrance could be to avoid being transported upstream by the strong flood currents, as it is apparent larval clinids are not very tolerant to low salinities (no larval clinids were caught <25 PSU). The distribution of larval clinids in the Tamar Estuary parallels that in estuaries in South Africa, where clinids occurred mainly in the euhaline region (30-36 PSU) (Strydom *et al.*, 2003). However, even though larval clinids may not tolerate low salinities, they did not show any evident tidal or diel behaviour, and their concentrations could not be accurately predicted by the estuarine transport model.

Moreover, no tidal/diel pattern was reported by Gunn and Thresher (Gunn and Thresher, 1991), in their detailed reproduction study of several Tasmanian clinids.

The lack of tidal/diel pattern of larval clinids, as well as their confined distribution within the lower Tamar Estuary could be mirroring the distribution of adults, as most species are live bearer and would occur around rocky and weedy reefs areas located in the lower reaches of the estuary (Last *et al.*, 1983; Gomon *et al.*, 1994). This view is supported by the fact that the transport model was unable to accurately predict the concentrations of clinids, thus suggesting that settlement habitats are close to the source of larvae which will affect model predictions (Brown *et al.*, 2005).

Engraulis australis

Larval anchovy (*E. australis*) were the fourth most abundant taxa during this study. Their highest concentrations were obtained in regions 30-40 km upstream during November both in 2001 and 2002. The proportion of anchovy larvae caught along the middle and upper estuary was ~10% higher than the lower estuary. The spatial distribution of anchovy larvae within the Tamar Estuary parallels that in other temperate estuaries in Australia, where high larval anchovy concentrations have been recorded in the middle and upper reaches (Arnott and McKinnon, 1985; Neira *et al.*, 1992; Neira and Potter, 1992a,b, 1994; Newton, 1996). This also implies that anchovy larvae have a high tolerance to salinity changes (Newton, 1996; Neira *et al.*, 1998).

Three main strategies used by anchovies to remain within the Tamar Estuary could be identified, namely upstream location, short spawning period and change in the vertical distribution of larvae along the water column.

The relative short occurrence of larval anchovy in the Tamar Estuary together with the significant relationship between zooplankton biomass and larval concentrations suggests that the spawning season of the anchovy is closely related to the food production cycle in the estuary. This short occurrence of larval anchovy in the Tamar, contrasts the situation in other estuaries where the occurrence of larval anchovy lasts >2 months indicating anchovy spawn over protracted periods of time (Leis and Rennis, 1983; Miller, 1984; Beckley, 1985; Neira *et al.*, 1992; Newton, 1996).

The high concentrations of larval anchovy found upstream could probably reflect the existence of a breeding population in this region. Anchovy populations are known to be capable of completing their life cycles within estuaries, as it has been observed in temperate Australian estuaries, but also around the coastal areas (Blackburn, 1950; Arnott and McKinnon, 1985). For those populations that breed inside estuaries, the upstream location of larval anchovy could help reduce their early loss from the system by giving them enough time, >25 days according to the transport model, to develop and improve their swimming ability. This also enables preflexion larvae to take advantage of the abundant food supply existing in the Tamar, as their ability to search for food is poor (Newton, 1996).

The distribution of flexion and postflexion anchovy larvae along the deeper (10-20) stratum in the lower estuary indicates an improvement in their swimming ability with larvae able to maintain their vertical position in order to avoid the strong surface currents (Ippen, 1966). In addition, diel and tidal patterns in larval anchovy concentrations became evident by February 2002, with the transport model unable to

accurately predict concentrations during this month. Their vertical distribution along the water column as well as a change in their behaviour and swimming ability will aid anchovy larvae to remain in the Tamar for as long as possible.

7.7 Conclusions

Although larval fish assemblages in the Tamar Estuary are typical of temperate estuaries, and several aspects of the larval fish dynamics are similar to those exhibited by larval fishes in estuaries worldwide, important differences occur between this highly-flushed system and estuaries characterized by weaker tidal currents. These include the lack of a distinct spatial distribution of larval fishes and zooplankton biomass, a lack of a distinct assemblage at the lower estuary, a stronger diel than tidal pattern in the distribution of larvae, and a short intensive larval production period strongly linked to the zooplankton productivity. The clear match between the occurrence of larval fishes and the cycle in zooplankton biomass perhaps reflects one of the most important strategies utilised by estuarine fish species in the Tamar: a well-timed spawning period, which will guarantee an appropriate food supply for larval fishes. This is particularly important at an early stage, as small larvae are less efficient at finding food and starvation is a far greater problem for them than for larger competent larvae (Gunn and Thresher, 1991). Another key strategy used by larvae in the highly-flushed Tamar Estuary appears to be spawning location: larvae spawned in the middle/upper reaches have greater chances of remaining within the estuary than larvae spawned in the lower reaches and or near the entrance, unless the latter employ additional strategies to avoid being flushed out. The location is particularly important in the case of early larvae and in taxa whose larvae have limited tolerance to salinity

changes, such as clinids and blenniids. Other strategies employed by larvae could be to enter the Tamar Estuary as early juveniles, such as flathead, Australian salmon or yellow eye mullet, or to remain along the estuary banks, such as atherinids (Boehlert and Mundy, 1988; Trnski, 2002).

Results of this thesis support in part the hypothesis set out for this study. Although the strategies employed by larvae in the Tamar Estuary are not quite overly different from those utilized by larvae in estuaries with weaker tidal currents, the variations observed could be of high value for the survival of larvae within this highly-flushed system. Strategies followed by estuarine-dependent fishes in the Tamar could therefore be summarized in a few words: "spawn hard, eat lots and grow fast, or otherwise die young".

7.8 References

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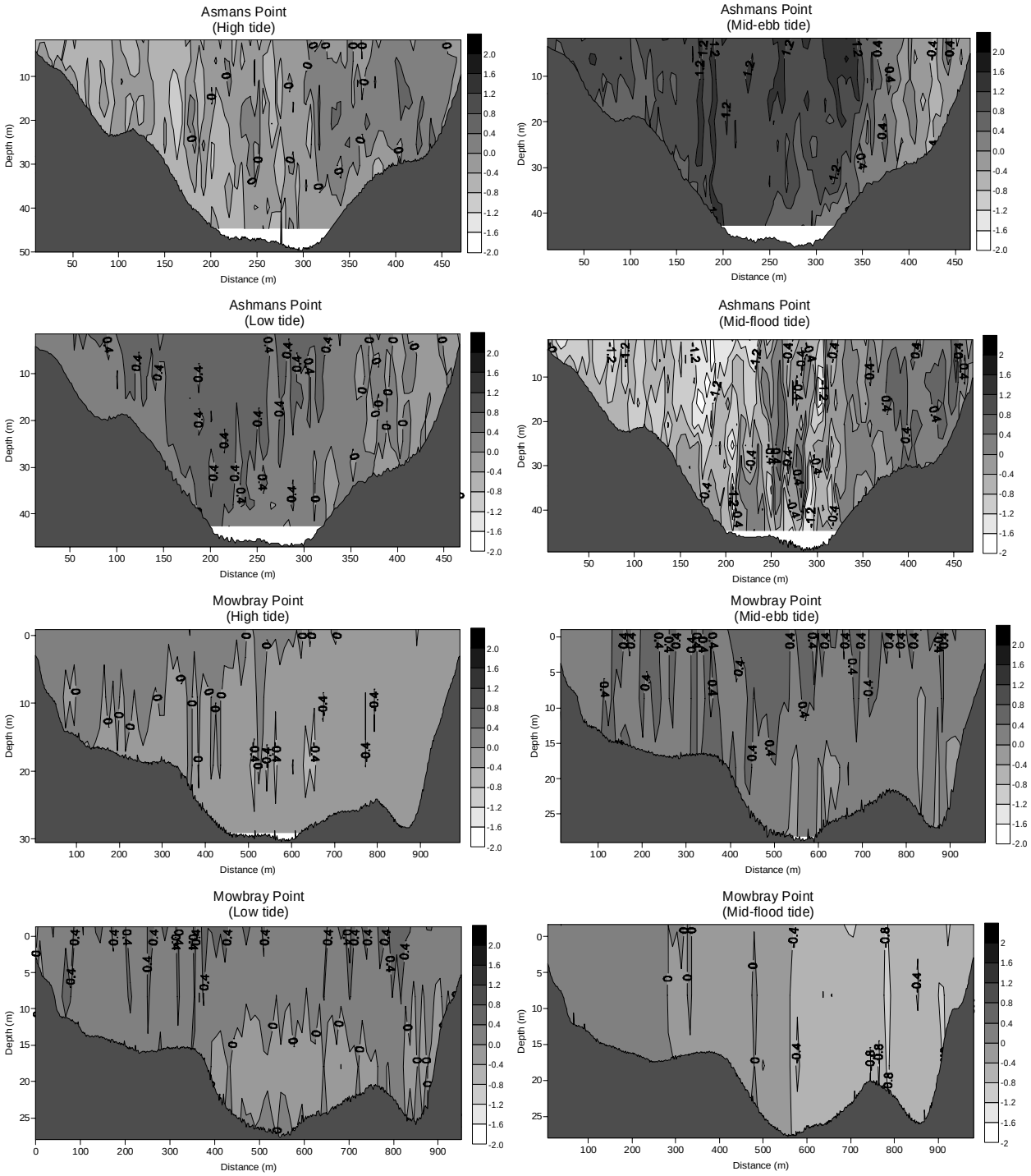
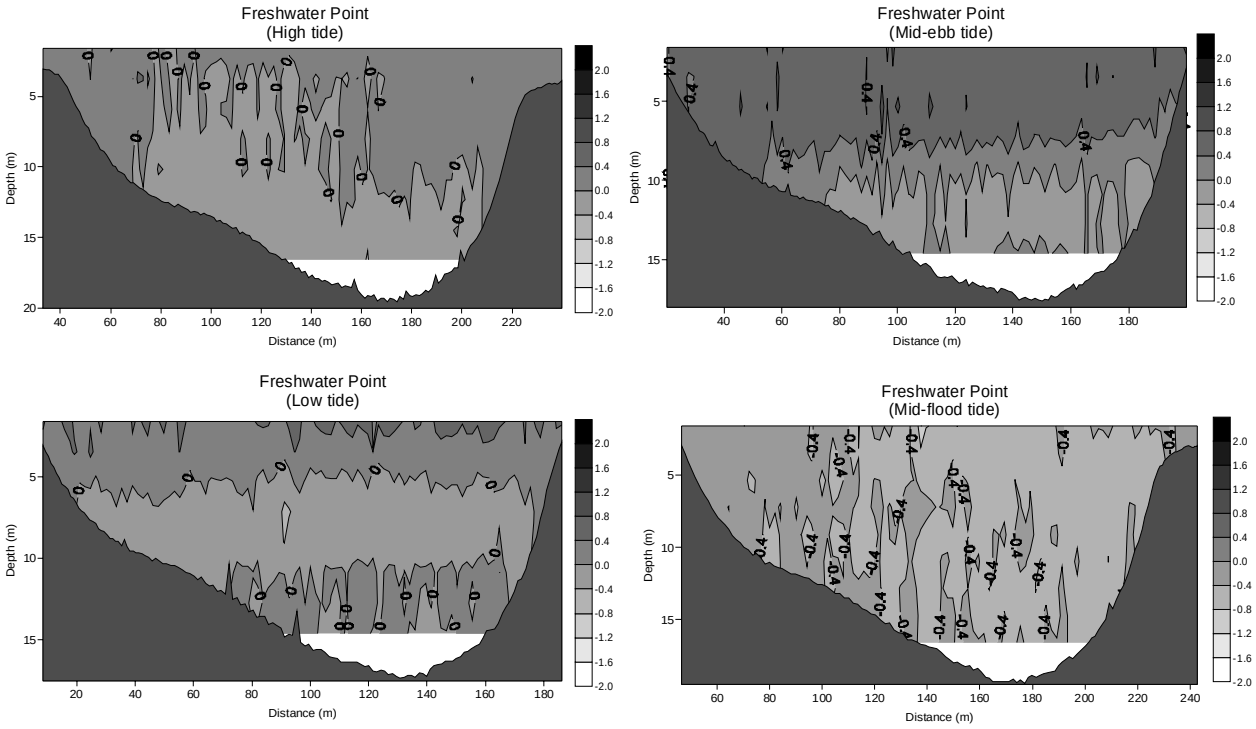
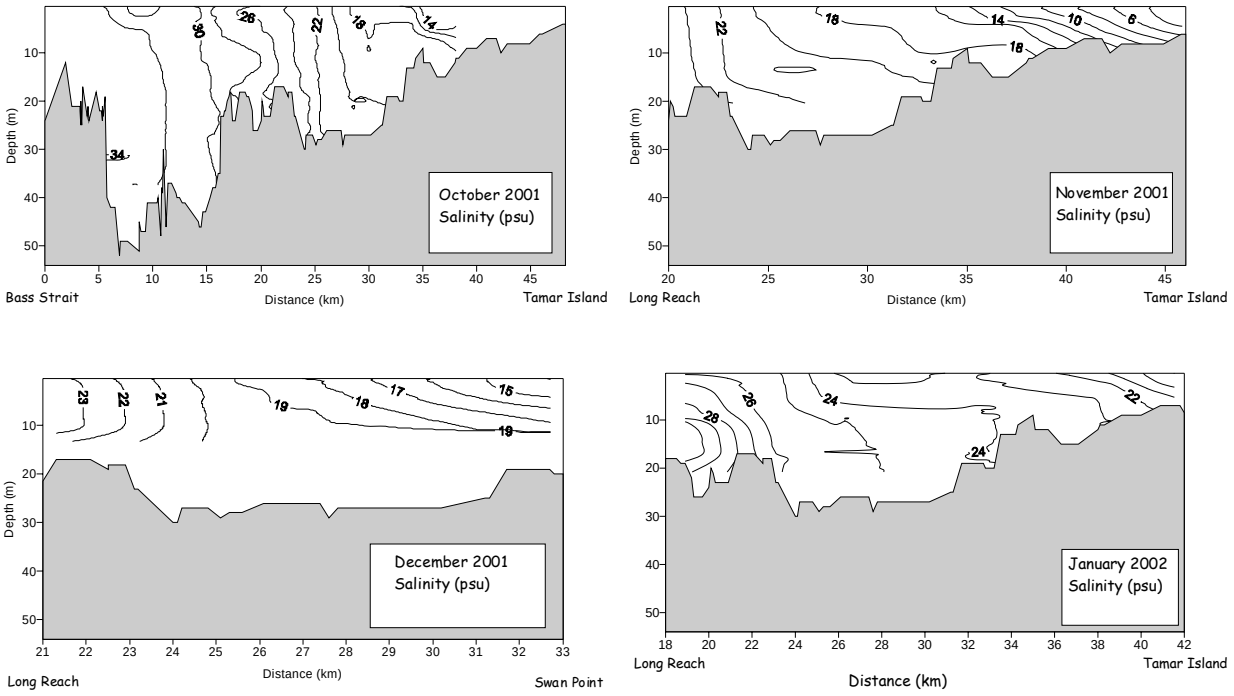
Appendix

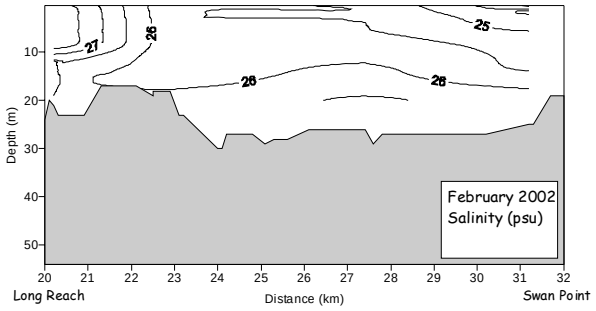
A.1 Velocity cross section profiles of high, mid-ebb/flood and low tide during spring tide at Ashmans Point, Mowbray Point and Freshwater Point. Negative values represent flood tide and positive values ebb tide.

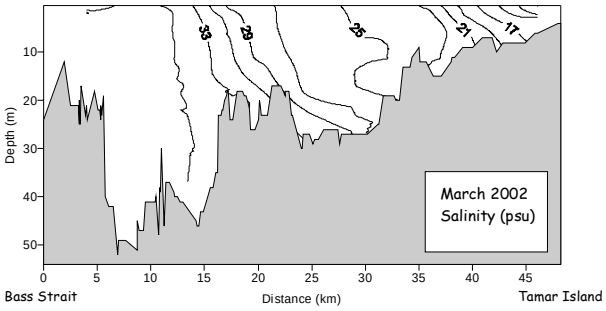


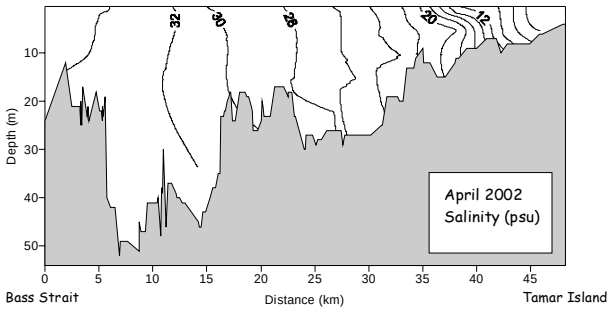


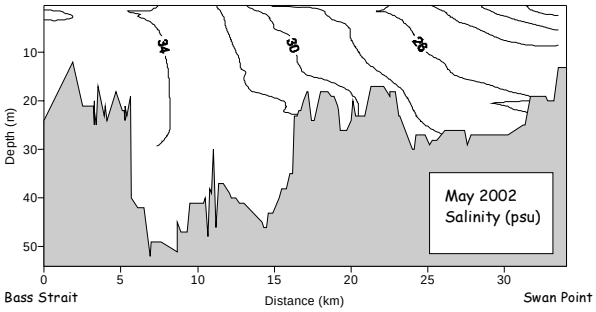
A.2 Vertical profiles of salinity obtained during routine sampling carried out throughout the Tamar Estuary between October 2001 and November 2002.

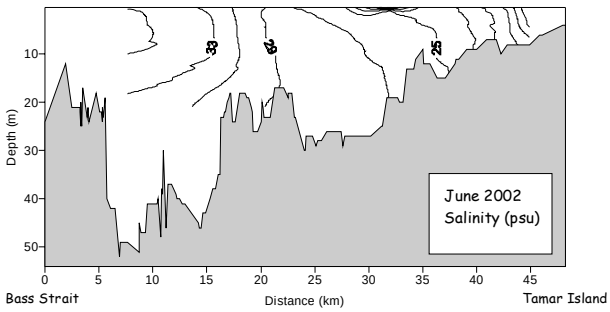


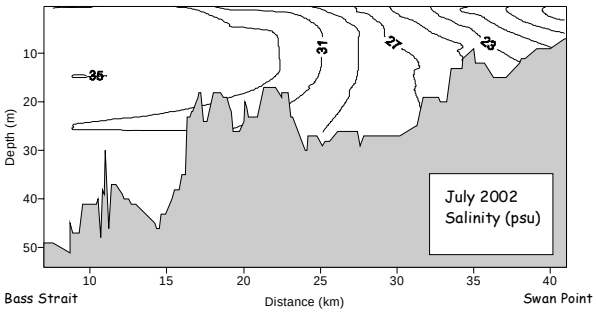

February 2002
Salinity (psu)
Depth (m)
Distance (km)
Long Reach
Swan Point

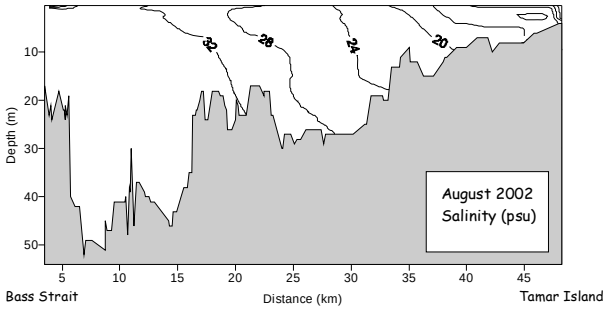

March 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Tamar Island

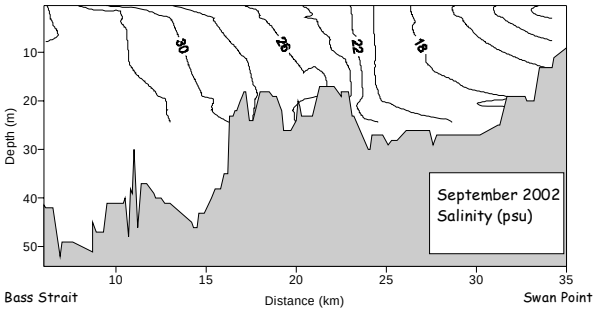

April 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Tamar Island

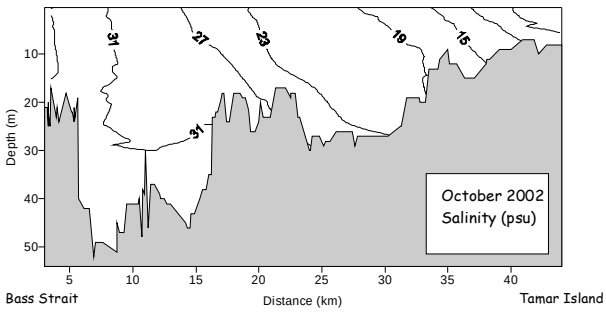

May 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Swan Point

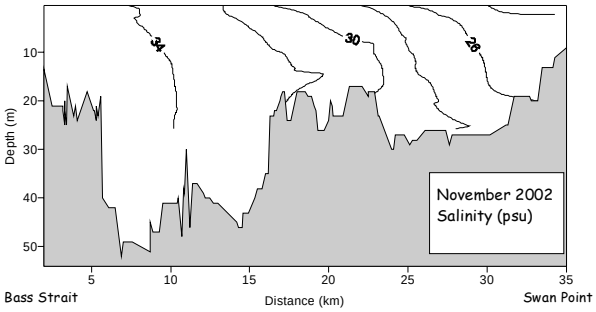

June 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Tamar Island


July 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Swan Point

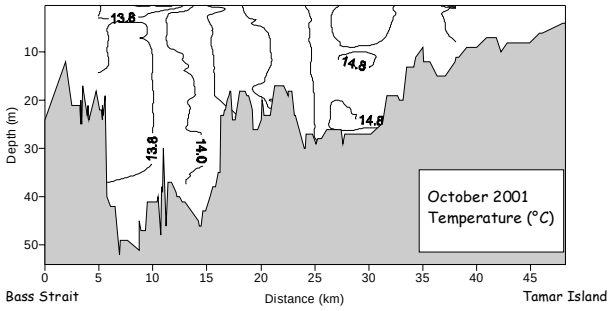

August 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Tamar Island

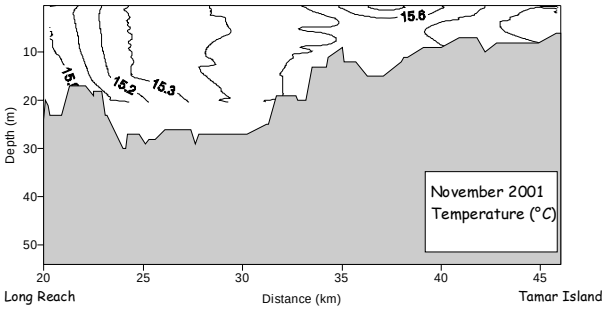

September 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Swan Point

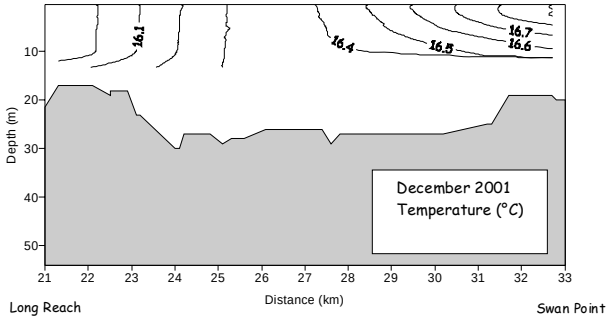

October 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Tamar Island

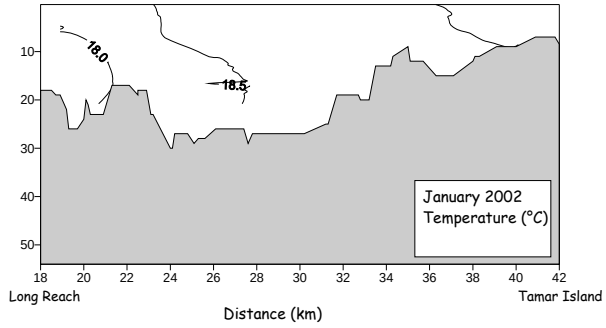

November 2002
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Swan Point

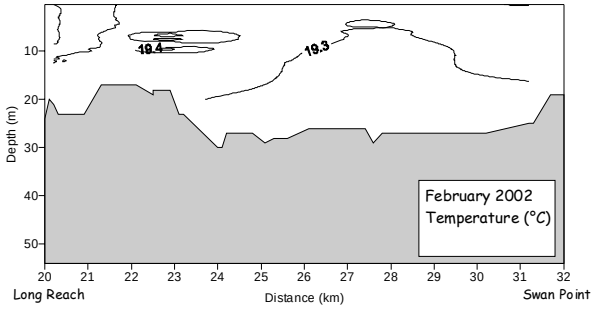
A.3 Vertical profiles of temperature obtained during routine sampling carried out throughout the Tamar Estuary between October 2001 and November 2002.

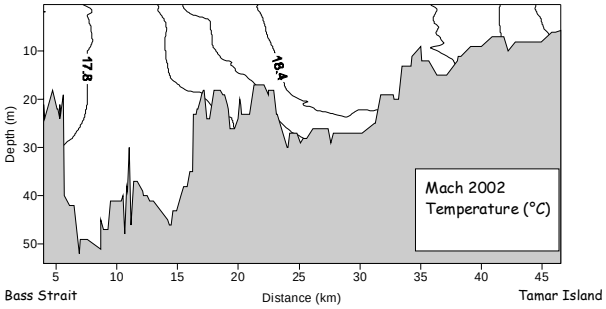


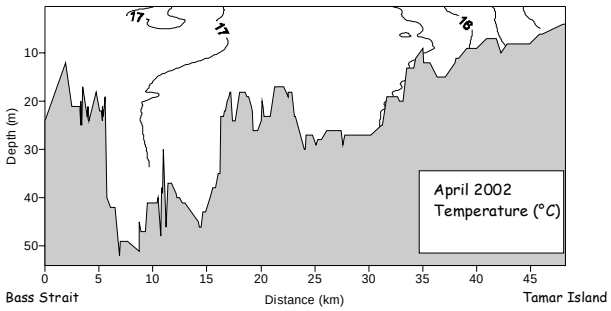


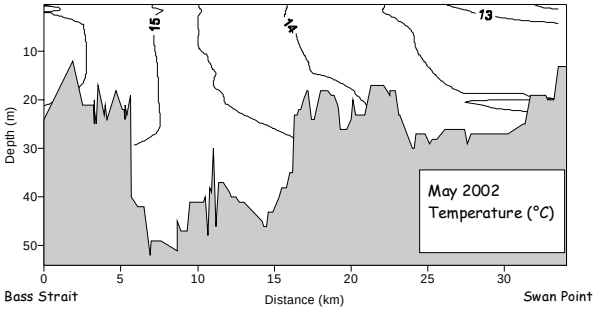


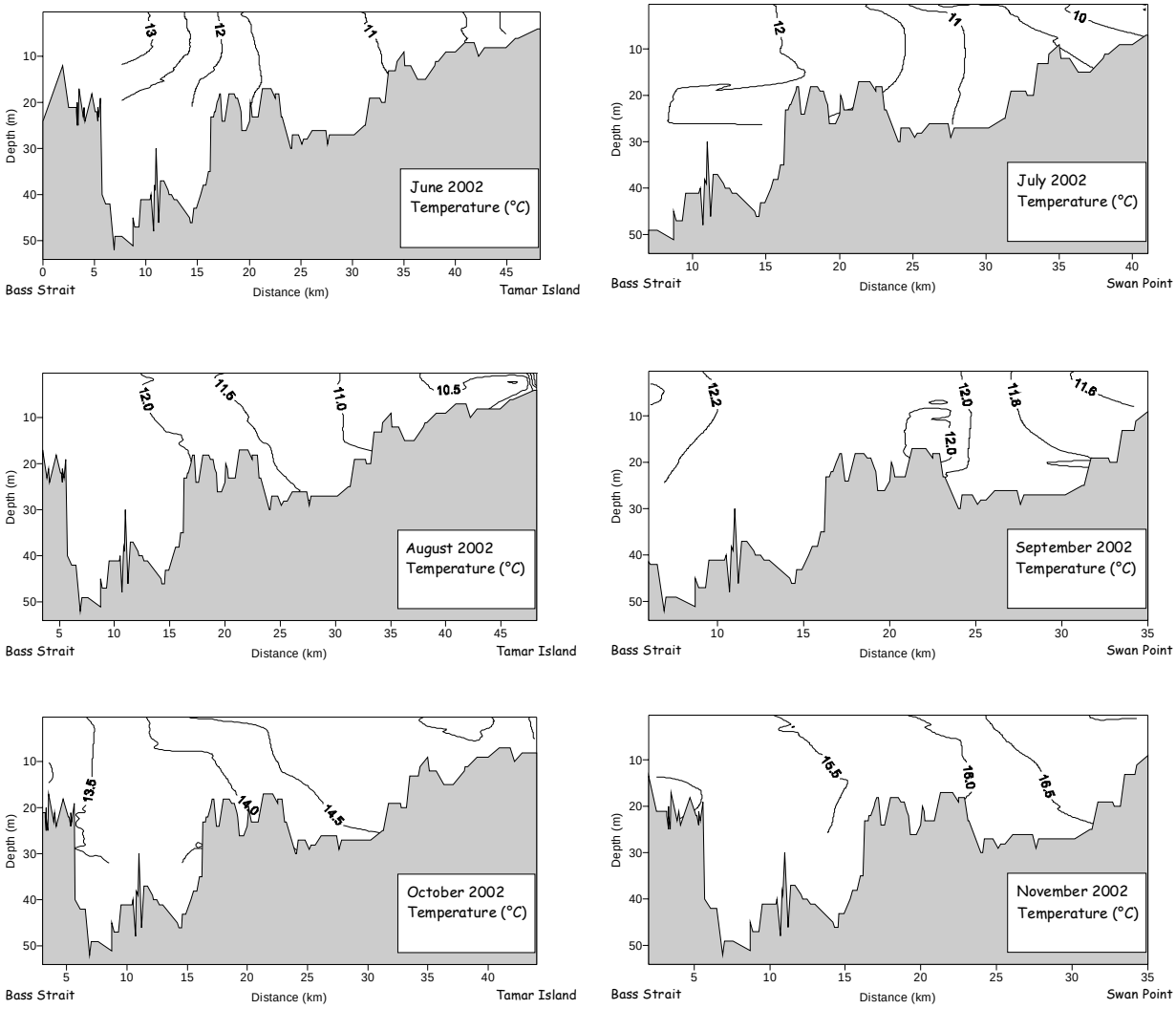




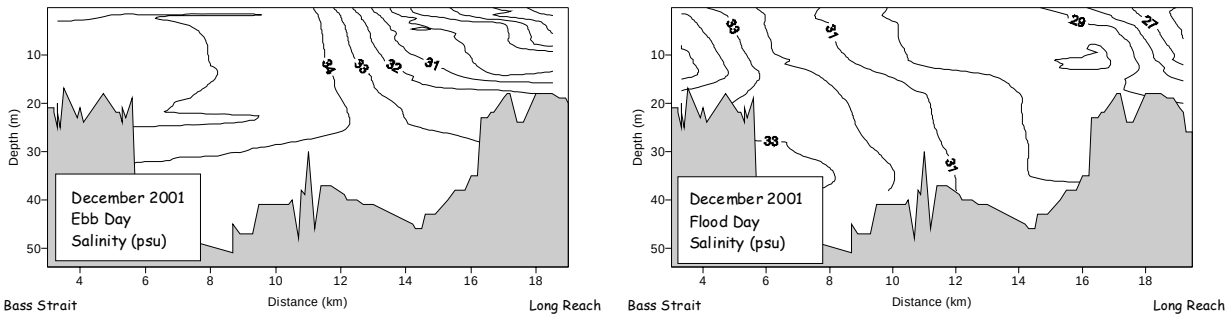


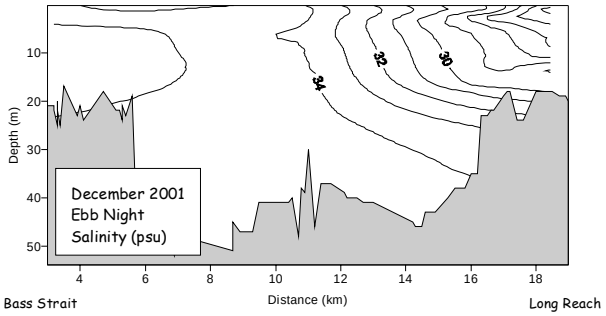


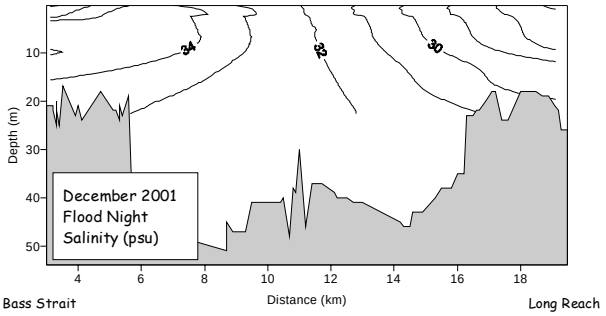


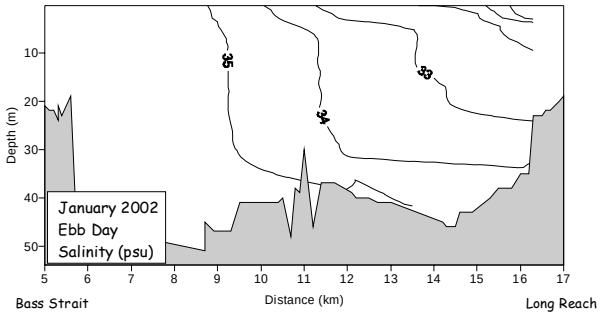


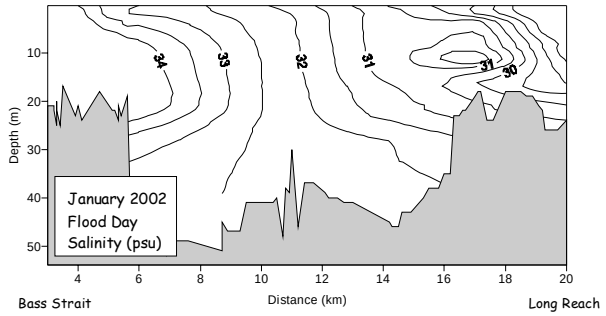
A.4 Vertical profiles of salinity obtained during 24-hour sampling regime carried out at the lower Tamar Estuary between December 2001 and February 2002.

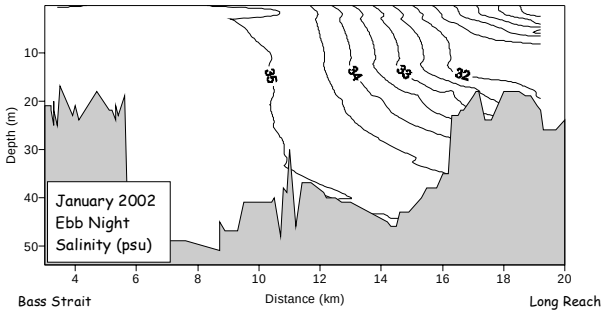


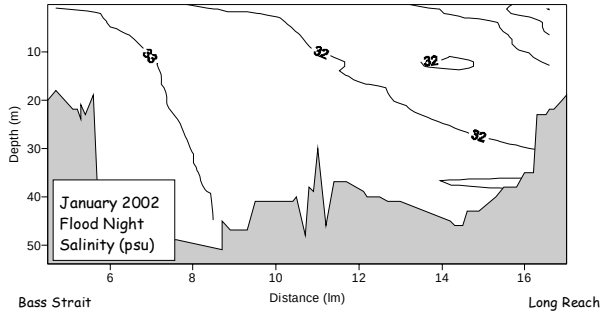

December 2001
Ebb Night
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach

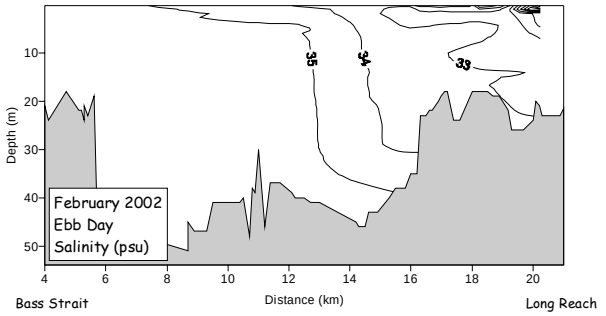

December 2001
Flood Night
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach

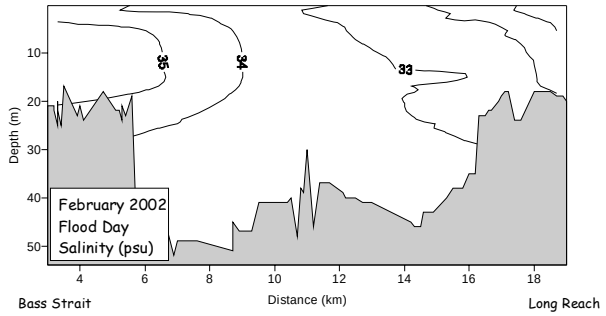

January 2002
Ebb Day
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach

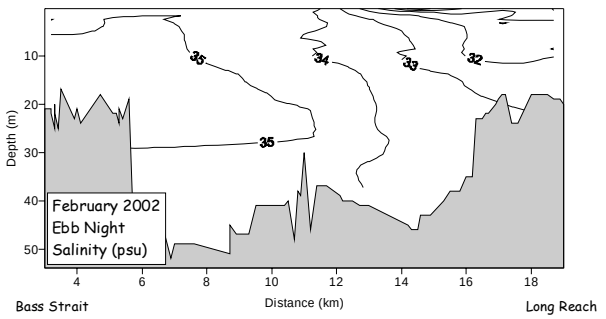

January 2002
Flood Day
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach

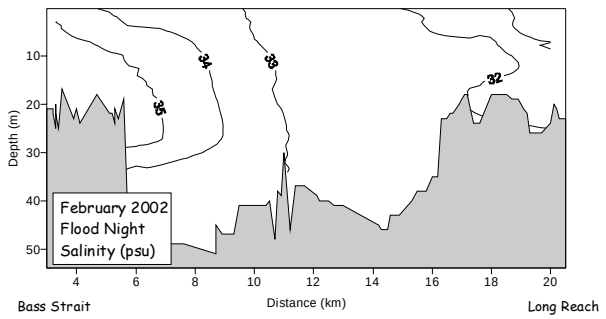

January 2002
Ebb Night
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach


January 2002
Flood Night
Salinity (psu)
Depth (m)
Distance (lm)
Bass Strait
Long Reach

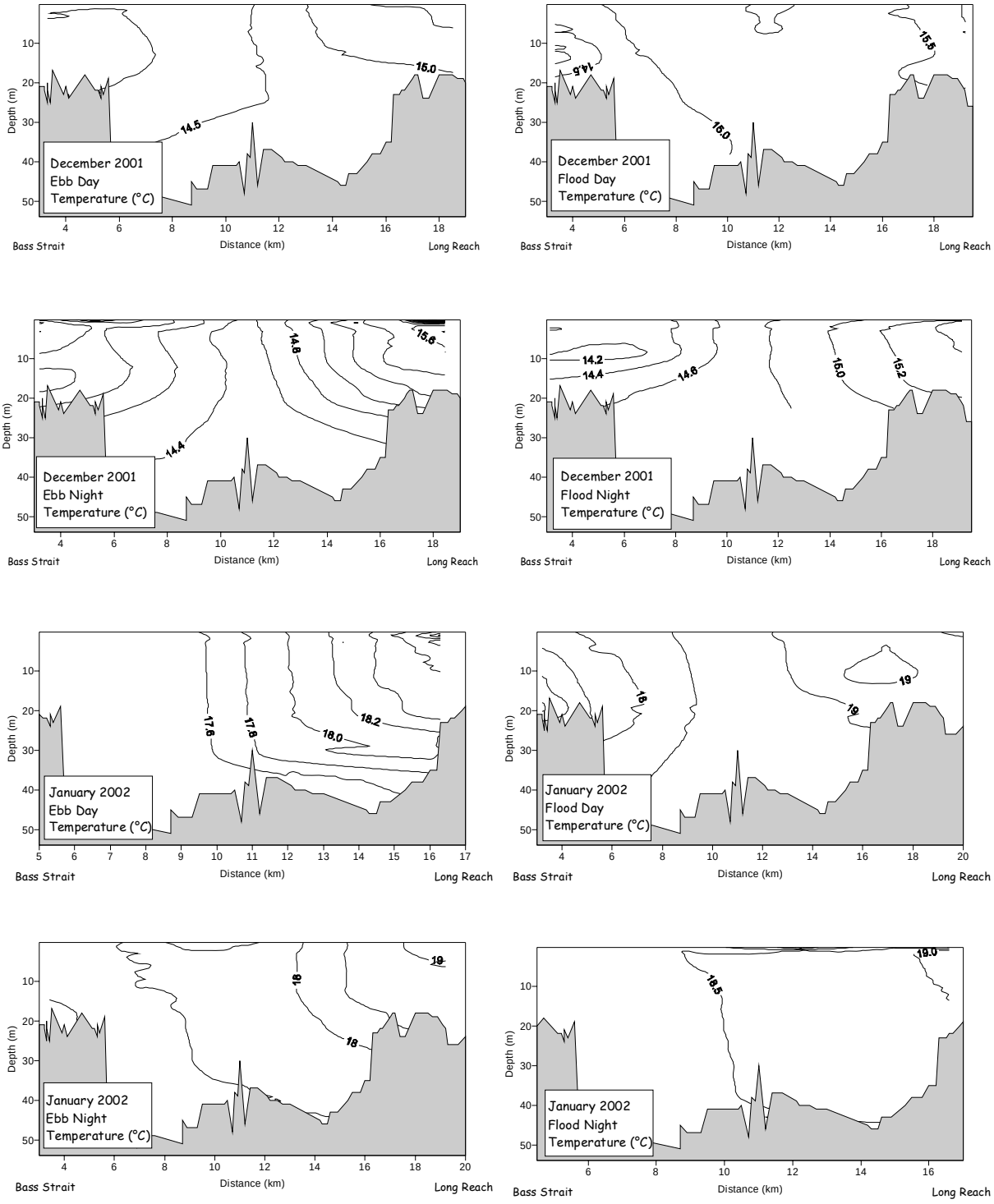

February 2002
Ebb Day
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach

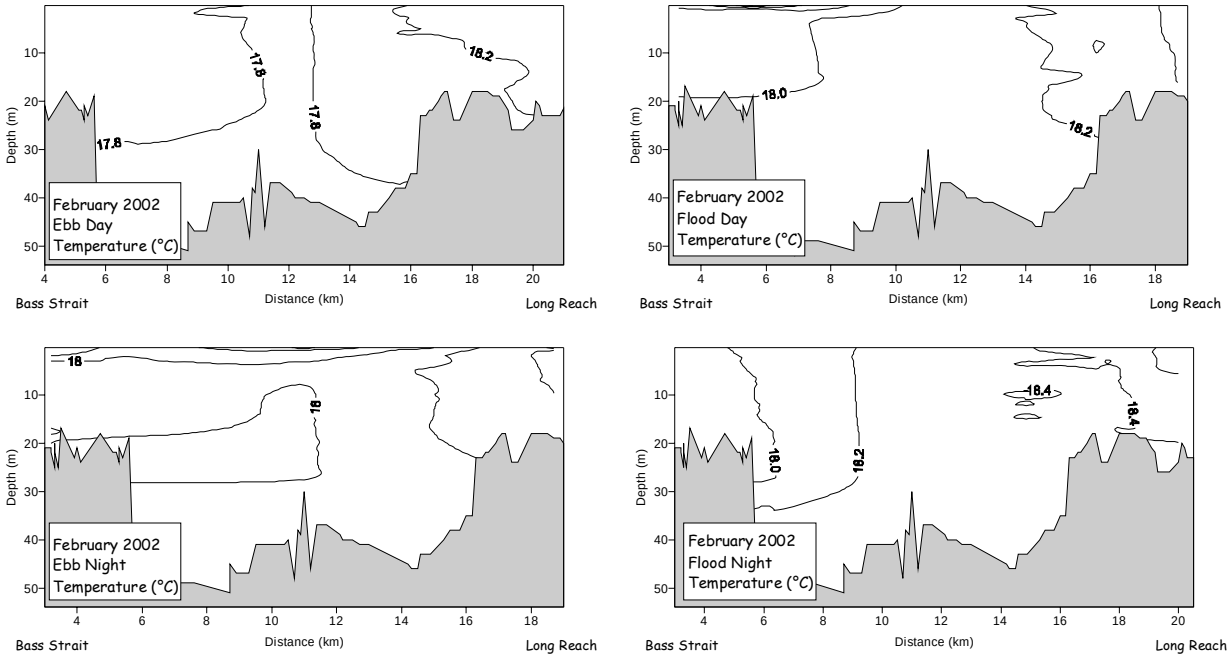

February 2002
Flood Day
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach


February 2002
Ebb Night
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach

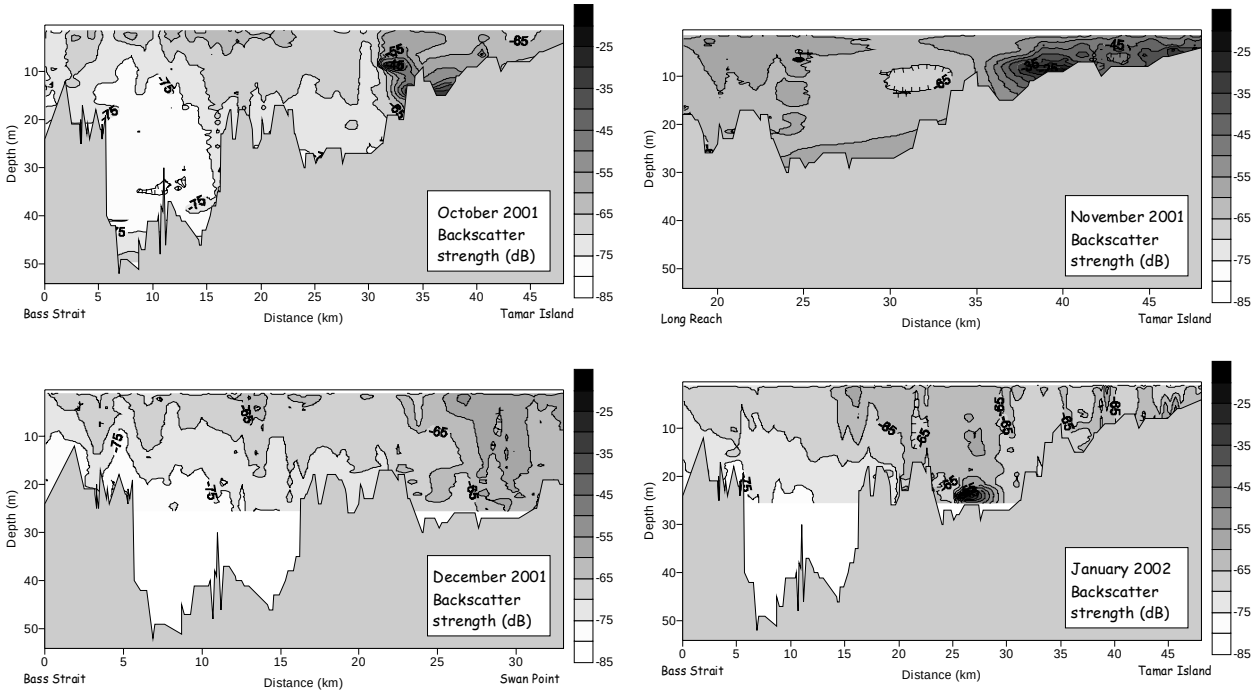

February 2002
Flood Night
Salinity (psu)
Depth (m)
Distance (km)
Bass Strait
Long Reach

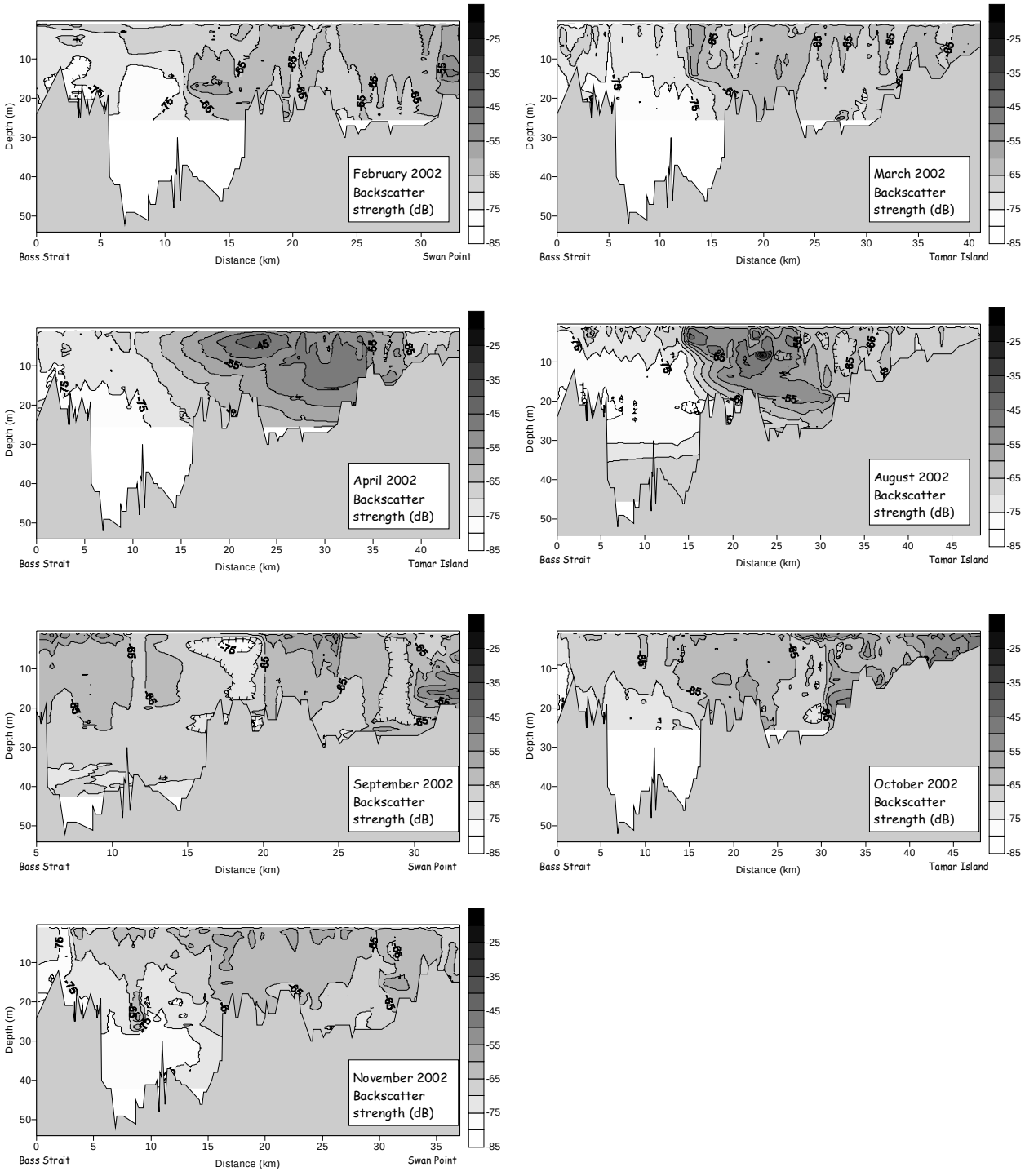
A.5 Vertical profiles of temperature obtained during 24-hour sampling regime carried out at the lower Tamar Estuary between December 2001 and February 2002.





A.6 Vertical profiles of backscatter strength obtained during routine sampling carried out throughout the Tamar Estuary between October 2001 - April 2002, and August – November 2002.




February 2002
Backscatter
strength (dB)
March 2002
Backscatter
strength (dB)
April 2002
Backscatter
strength (dB)
August 2002
Backscatter
strength (dB)
September 2002
Backscatter
strength (dB)
October 2002
Backscatter
strength (dB)
November 2002
Backscatter
strength (dB)
Depth (m)
Distance (km)
Bass Strait
Swan Point
Tamar Island
-25
-35
-45
-55
-65
-75
-85

A.7 Descriptive statistics of monthly means for temperature (°C), salinity (PSU) and freshwater flow (m^3/s) data obtained during routine sampling carried out throughout the Tamar Estuary between October 2001 and November 2002. Abbreviations: SD, standard deviation; SE, standard error, CI, confidence intervals.

Month	Mean	SD	n	SE	CI	Mean	SD	n	SE	CI
Temperature						**Freshwater flow (South Esk)**				
O-01	14.27	0.56	15	0.15	0.31	123.28	50.26	30	9.18	18.74
N-01	15.38	0.23	6	0.09	0.22	100.97	60.46	30	11.04	22.54
D-01	15.71	0.75	10	0.24	0.53	65.18	19.85	31	3.56	7.27
J-02	18.61	0.71	12	0.20	0.44	48.14	9.02	31	1.62	3.30
F-02	18.66	0.65	9	0.22	0.49	57.21	9.77	28	1.85	3.78
M-02	18.18	0.30	10	0.09	0.21	53.32	13.97	30	2.55	5.21
A-02	16.47	0.77	10	0.24	0.54	52.82	5.34	30	0.97	1.99
M-02	14.20	0.92	8	0.32	0.75	58.00	5.37	31	0.96	1.97
J-02	11.39	1.05	11	0.32	0.70	53.37	18.76	30	3.43	7.00
J-02	11.16	0.92	8	0.32	0.75	40.99	18.84	31	3.38	6.90
A-02	11.11	1.11	11	0.34	0.74	57.34	22.18	31	3.98	8.12
S-02	12.01	0.29	7	0.11	0.25	119.18	41.16	30	7.51	15.35
O-02	14.28	0.68	10	0.21	0.48	79.23	25.75	31	4.63	9.43
N-02	16.10	0.69	7	0.26	0.62	25.82	9.78	30	1.79	3.65
Salinity						**Freshwater flow (North Esk)**				
O-01	25.96	7.20	15	1.86	3.96	16.85	6.59	31	1.18	2.41
N-01	16.95	7.54	6	3.08	7.53	13.83	7.69	30	1.40	2.87
D-01	25.93	6.72	10	2.13	4.74	7.60	2.71	31	0.49	0.99
J-02	28.04	5.04	12	1.46	3.17	5.54	2.96	31	0.53	1.08
F-02	30.29	4.10	9	1.37	3.09	3.10	1.99	28	0.38	0.77
M-02	27.88	6.69	10	2.12	4.72	1.12	0.25	31	0.05	0.09
A-02	23.95	10.30	10	3.26	7.26	0.83	0.39	30	0.07	0.14
M-02	29.67	4.60	8	1.63	3.75	1.55	1.55	31	0.28	0.57
J-02	27.02	6.47	11	1.95	4.30	16.94	5.64	30	1.03	2.10
J-02	28.61	6.56	8	2.32	5.35	5.93	10.58	31	1.90	3.87
A-02	24.30	10.94	11	3.30	7.26	14.78	8.76	31	1.57	3.21
S-02	24.25	7.78	7	2.94	6.95	33.07	15.07	30	2.75	5.62
O-02	21.14	10.48	10	3.31	7.38	19.49	9.69	31	1.74	3.55
N-02	29.78	4.14	7	1.56	3.70	5.67	2.16	30	0.39	0.80

A.8 Descriptive statistics of monthly means for zooplankton biomass (g/100 m^3) and larval fish concentrations (numbers/100 m^3) collected during routine sampling carried out throughout the Tamar Estuary between October 2001 and November 2002. Abbreviations: SD, standard deviation; SE, standard error, CI, confidence intervals.

Month	Mean	SD	n	SE	CI
Biomass					
O-01	1.64	1.02	20	0.23	0.48
N-01	4.06	3.72	12	1.07	2.34
D-01	1.10	0.29	6	0.12	0.29
J-02	0.23	0.15	12	0.04	0.10
F-02	0.83	0.82	4	0.41	1.13
M-02	0.64	0.37	12	0.11	0.23
A-02	0.46	0.53	18	0.12	0.26
M-02	0.10	0.08	12	0.02	0.05
J-02	0.31	0.34	18	0.08	0.17
J-02	0.07	0.07	12	0.02	0.05
A-02	0.30	0.31	18	0.07	0.15
S-02	0.45	0.28	12	0.08	0.17
O-02	1.06	1.48	18	0.35	0.74
N-02	1.15	1.24	12	0.36	0.78
Larval fish concentrations					
O-01	137.62	107.82	20	24.11	50.46
N-01	540.98	487.60	12	140.76	309.81
D-01	336.87	334.45	12	96.55	212.50
J-02	16.77	16.80	18	3.96	8.35
F-02	15.34	18.97	10	6.00	13.57
M-02	1.93	1.49	12	0.43	0.95
A-02	4.17	2.64	18	0.62	1.31
M-02	1.57	1.68	12	0.49	1.07
J-02	0.70	0.84	18	0.20	0.42
J-02	2.26	2.44	12	0.70	1.55
A-02	27.01	54.45	18	12.83	27.08
S-02	28.55	22.40	12	6.47	14.23
O-02	211.08	226.34	18	53.35	112.55
N-02	762.70	624.42	12	180.26	396.74

A.9 Descriptive statistics of monthly means for zooplankton biomass (g/100 m^3) and larval fish concentrations (numbers/100 m^3) at each of the Venice salinity regions obtained during routine sampling carried out throughout the Tamar Estuary between October 2001 and November 2002. Abbreviations: SD, standard deviation; SE, standard error, CI, confidence intervals.

Month	Mean	SD	n	SE	CI	Mean	SD	n	SE	CI
Zooplankton biomass						**Larval fishes**				
Euhaline										
O-01	1.75	1.53	6.00	0.63	1.53	209.31	112.92	6	46.10	118.50
N-01	-	-	-	-	-	-	-	-	-	-
D-01	-	-	-	-	-	167.80	42.35	2	29.94	380.47
J-02	-	-	-	-	-	21.60	17.20	4	8.60	27.37
F-02	-	-	-	-	-	22.67	21.92	6	8.95	23.01
M-02	0.76	0.39	6.00	0.16	0.39	2.36	1.30	6	0.53	1.37
A-02	0.57	0.60	6.00	0.24	0.59	3.25	2.64	6	1.08	2.77
M-02	0.15	0.08	6.00	0.03	0.08	1.51	1.61	6	0.66	1.69
J-02	0.44	0.24	6.00	0.10	0.24	0.79	0.55	6	0.23	0.58
J-02	0.10	0.09	6.00	0.04	0.09	3.19	2.86	6	1.17	3.00
A-02	0.66	0.25	6.00	0.10	0.25	17.74	5.70	6	2.33	5.99
S-02	0.69	0.26	4.00	0.13	0.36	37.37	16.90	4	8.45	26.90
O-02	2.20	2.22	6.00	0.91	2.22	350.33	284.82	6	116.28	298.90
N-02	0.57	0.15	6.00	0.06	0.15	651.23	609.22	6	248.71	639.34
Polyhaline										
O-01	1.62	0.88	10.00	0.28	0.62	129.61	101.42	10	32.07	72.55
N-01	2.07	2.38	6.00	0.97	2.38	681.13	359.82	6	146.90	377.61
D-01	0.99	0.10	4.00	0.05	0.14	435.73	375.26	8	132.68	313.73
J-02	0.24	0.15	10.00	0.05	0.11	16.21	18.38	12	5.31	11.68
F-02	0.83	0.82	4.00	0.41	1.13	4.34	3.17	4	1.59	5.05
M-02	0.52	0.33	6.00	0.14	0.33	1.50	1.66	6	0.68	1.74
A-02	0.69	0.61	6.00	0.25	0.60	3.12	1.90	6	0.78	1.99
M-02	0.04	0.03	6.00	0.01	0.03	1.63	1.90	6	0.78	2.00
J-02	0.11	0.09	10.00	0.03	0.06	0.37	0.52	10	0.17	0.37
J-02	0.04	0.03	6.00	0.01	0.03	1.32	1.68	6	0.69	1.77
A-02	0.18	0.04	6.00	0.02	0.04	4.69	1.92	6	0.78	2.01
S-02	0.43	0.11	6.00	0.05	0.11	32.03	23.24	6	9.49	24.39
O-02	0.70	0.27	6.00	0.11	0.27	251.92	166.66	6	68.04	174.90
N-02	1.73	1.59	6.00	0.65	1.59	874.18	675.88	6	275.93	709.29

A.9 *Continued*

Month	Mean	SD	n	SE	CI	Mean	SD	n	SE	CI
Zooplankton biomass						**Larval fishes**				
Mesohaline										
O-01	1.51	0.58	4.00	0.29	0.81	50.09	28.54	4	14.27	45.41
N-01	6.29	3.66	4.00	1.83	5.08	552.64	696.57	4	348.28	1108.40
D-01	1.33	0.47	2.00	0.33	1.44	110.54	71.36	2	50.46	641.18
J-02	0.21	0.21	2.00	0.15	1.90	10.50	4.11	2	2.91	36.92
F-02	-	-	-	-	-	-	-	-	-	-
M-02	-	-	-	-	-	-	-	-	-	-
A-02	0.12	0.07	6.00	0.03	0.07	6.13	2.47	6	1.01	2.59
M-02	-	-	-	-	-	-	-	-	-	-
J-02	0.92	0.57	2.00	0.40	1.72	2.07	1.74	2	1.23	15.64
J-02	-	-	-	-	-	-	-	-	-	-
A-02	0.02	0.02	4.00	0.01	0.03	2.71	4.40	4	2.20	7.01
S-02	0.03	0.04	2.00	0.03	0.11	0.45	0.64	2	0.45	5.73
O-02	0.29	0.26	6.00	0.11	0.26	31.00	33.05	6	13.49	34.69
N-02	-	-	-	-	-	-	-	-	-	-
Oligohaline										
O-01	-	-	-	-	-	-	-	-	-	-
N-01	5.56	5.97	2.00	4.22	18.17	97.20	4.22	2	2.98	37.89
D-01	-	-	-	-	-	-	-	-	-	-
J-02	-	-	-	-	-	-	-	-	-	-
F-02	-	-	-	-	-	-	-	-	-	-
M-02	-	-	-	-	-	-	-	-	-	-
A-02	-	-	-	-	-	-	-	-	-	-
M-02	-	-	-	-	-	-	-	-	-	-
J-02	-	-	-	-	-	-	-	-	-	-
J-02	-	-	-	-	-	-	-	-	-	-
A-02	0.08	0.03	2.00	0.02	0.10	170.42	56.21	2	39.75	505.01
S-02	-	-	-	-	-	-	-	-	-	-
O-02	-	-	-	-	-	-	-	-	-	-
N-02	-	-	-	-	-	-	-	-	-	-

A.10 Descriptive statistics of monthly means for Gobiidae, Blenniidae, Clinidae and Engraulidae concentrations (numbers/100 m^3) obtained during routine sampling carried out throughout the Tamar Estuary between October 2001 and November 2002. Abbreviations: SD, standard deviation; SE, standard error, CI, confidence intervals.

Month	Mean	SD	n	SE	CI	Month	Mean	SD	n	SE
Gobiidae						**Clinidae**				
O-01	47.18	51.34	20	11.48	24.03	10.77	15.17	20	3.39	7.10
N-01	481.21	445.40	12	128.57	282.99	0.89	1.95	12	0.56	1.24
D-01	260.71	342.68	12	98.92	217.73	28.02	24.87	12	7.18	15.80
J-02	2.41	1.84	18	0.43	0.92	3.59	6.99	18	1.65	3.48
F-02	0.84	1.28	10	0.41	0.92	6.06	10.28	10	3.25	7.35
M-02	0.16	0.29	12	0.08	0.19	0.05	0.17	12	0.05	0.11
A-02	0.30	0.56	18	0.13	0.28	-	-	-	-	-
M-02	0.05	0.17	10	0.05	0.12	-	-	-	-	-
J-02	0.14	0.30	14	0.08	0.17	0.09	0.23	14	0.06	0.14
J-02	0.32	0.68	10	0.22	0.49	0.15	0.24	10	0.08	0.17
A-02	18.56	50.75	18	11.96	25.24	0.15	0.30	18	0.07	0.15
S-02	12.34	12.70	12	3.67	8.07	2.16	2.24	12	0.65	1.42
O-02	195.97	231.37	18	54.53	115.06	2.92	5.69	18	1.34	2.83
N-02	597.93	638.10	12	184.20	405.43	20.66	21.45	12	6.19	13.63
Blenniidae						**Engraulidae**				
O-01	0.72	0.84	20	0.19	0.40	2.58	3.59	20	0.80	1.68
N-01	5.95	11.90	12	3.44	7.56	28.48	39.59	12	11.43	25.15
D-01	16.66	10.71	12	3.09	6.81	16.54	16.90	12	4.88	10.73
J-02	6.98	13.22	18	3.12	6.58	1.30	2.10	18	0.49	1.04
F-02	5.25	5.46	10	1.73	3.91	-	-	-	-	-
M-02	0.45	0.66	12	0.19	0.42	-	-	-	-	-
A-02	-	-	-	-	-	0.03	0.13	18	0.03	0.06
M-02	-	-	-	-	-	-	-	-	-	-
J-02	-	-	-	-	-	-	-	-	-	-
J-02	-	-	-	-	-	-	-	-	-	-
A-02	-	-	-	-	-	-	-	-	-	-
S-02	0.14	0.28	12	0.08	0.18	-	-	-	-	-
O-02	3.96	5.54	18	1.31	2.75	1.70	2.96	18	0.70	1.47
N-02	47.36	40.29	12	11.63	25.60	85.25	147.84	12	42.68	93.93

A.11 Descriptive statistics of means for temperature (°C), salinity (PSU) data obtained during the 24-hour sampling regime carried out at the lower Tamar Estuary between December 2001 and February 2002. Abbreviations: D-01, December 2001; J-02, January 2002; F-02, February 2002; SD, standard deviation; SE, standard error, CI, confidence intervals.

Month	Tide	Site	Mean	SD	n	SE	CI	Mean	SD	n	SE	CL
Salinity								**Temperature**				
D-01	ED	1	35.23	0.17	20.00	0.04	0.08	13.90	0.20	20.00	0.04	0.09
D-01	ED	2	35.31	0.19	16.00	0.05	0.10	13.89	0.15	16.00	0.04	0.08
D-01	ED	3	34.63	0.07	26.00	0.01	0.03	14.47	0.02	26.00	0.00	0.01
D-01	ED	4	32.04	1.29	38.00	0.21	0.42	14.97	0.22	38.00	0.04	0.07
D-01	ED	5	29.63	1.42	19.00	0.33	0.68	15.35	0.24	19.00	0.06	0.12
D-01	ED	6	27.95	1.49	14.00	0.40	0.86	15.58	0.22	14.00	0.06	0.13
D-01	EN	1	35.32	0.22	17.00	0.05	0.11	13.98	0.19	17.00	0.05	0.10
D-01	EN	2	35.19	0.33	15.00	0.08	0.18	14.01	0.16	15.00	0.04	0.09
D-01	EN	3	34.36	0.14	37.00	0.02	0.05	14.46	0.02	37.00	0.00	0.01
D-01	EN	4	28.99	1.00	20.00	0.22	0.47	15.41	0.12	20.00	0.03	0.05
D-01	EN	5	-	-	-	-	-	-	-	-	-	-
D-01	EN	6	27.14	1.51	15.00	0.39	0.83	15.49	0.49	15.00	0.13	0.27
D-01	FD	1	34.82	0.59	15.00	0.15	0.33	14.39	0.37	15.00	0.09	0.20
D-01	FD	2	32.56	0.70	37.00	0.12	0.23	14.95	0.15	37.00	0.02	0.05
D-01	FD	3	29.62	0.23	14.00	0.06	0.13	15.50	0.07	14.00	0.02	0.04
D-01	FD	4	29.94	0.14	39.00	0.02	0.04	15.41	0.01	39.00	0.00	0.00
D-01	FD	5	29.32	0.69	14.00	0.19	0.40	15.44	0.11	14.00	0.03	0.06
D-01	FD	6	26.77	0.87	17.00	0.21	0.45	15.89	0.14	17.00	0.03	0.07
D-01	FN	1	34.18	0.83	11.00	0.25	0.55	14.36	0.11	11.00	0.03	0.07
D-01	FN	2	34.88	0.07	10.00	0.02	0.05	14.21	0.03	10.00	0.01	0.02
D-01	FN	3	32.36	0.06	24.00	0.01	0.03	14.75	0.01	24.00	0.00	0.00
D-01	FN	4	-	-	-	-	-	-	-	-	-	-
D-01	FN	5	-	-	-	-	-	-	-	-	-	-
D-01	FN	6	28.46	0.72	17.00	0.17	0.37	15.43	0.06	17.00	0.01	0.03
J-02	ED	1	-	-	-	-	-	-	-	-	-	-
J-02	ED	2	35.34	0.04	34.00	0.01	0.01	17.49	0.02	34.00	0.00	0.01
J-02	ED	3	35.23	0.05	43.00	0.01	0.02	17.45	0.01	43.00	0.00	0.00
J-02	ED	4	33.65	0.30	32.00	0.05	0.11	18.02	0.08	32.00	0.01	0.03
J-02	ED	5	32.39	0.14	15.00	0.04	0.08	18.48	0.05	15.00	0.01	0.03
J-02	ED	6	31.72	0.86	22.00	0.18	0.38	18.70	0.21	22.00	0.05	0.09

A.11 *Continued*

Month	Tide	Site	Mean	SD	n	SE	CI	Mean	SD	n	SE	CL
Salinity								**Temperature**				
J-02	EN	1	35.28	0.11	25.00	0.02	0.04	17.08	0.21	25.00	0.04	0.09
J-02	EN	2	35.26	0.03	47.00	0.00	0.01	17.46	0.06	47.00	0.01	0.02
J-02	EN	3	34.94	0.04	35.00	0.01	0.01	17.55	0.02	35.00	0.00	0.01
J-02	EN	4	-	-	-	-	-	-	-	-	-	-
J-02	EN	5	31.42	0.36	15.00	0.09	0.20	18.89	0.03	15.00	0.01	0.02
J-02	EN	6	31.24	0.89	21.00	0.19	0.40	18.98	0.14	21.00	0.03	0.06
J-02	FD	1	35.16	0.24	21.00	0.05	0.11	17.12	0.42	21.00	0.09	0.19
J-02	FD	2	34.38	0.52	22.00	0.11	0.23	17.83	0.22	22.00	0.05	0.10
J-02	FD	3	32.31	0.07	40.00	0.01	0.02	18.73	0.02	40.00	0.00	0.01
J-02	FD	4	30.93	0.31	25.00	0.06	0.13	19.09	0.08	25.00	0.02	0.03
J-02	FD	5	31.05	0.66	13.00	0.18	0.40	19.02	0.14	13.00	0.04	0.08
J-02	FD	6	28.45	0.71	20.00	0.16	0.33	19.45	0.20	20.00	0.04	0.09
J-02	FN	1	-	-	-	-	-	-	-	-	-	-
J-02	FN	2	33.73	0.27	45.00	0.04	0.08	18.03	0.11	45.00	0.02	0.03
J-02	FN	3	32.71	0.16	46.00	0.02	0.05	18.44	0.04	46.00	0.01	0.01
J-02	FN	4	31.96	0.24	40.00	0.04	0.08	18.63	0.19	40.00	0.03	0.06
J-02	FN	5	31.58	0.43	14.00	0.11	0.24	18.78	0.06	14.00	0.02	0.04
J-02	FN	6	30.44	0.66	19.00	0.15	0.32	19.06	0.14	19.00	0.03	0.07
F-02	ED	1	35.33	0.04	19.00	0.01	0.02	17.85	0.02	19.00	0.01	0.01
F-02	ED	2	35.37	0.10	21.00	0.02	0.04	17.87	0.01	21.00	0.00	0.01
F-02	ED	3	35.09	0.17	41.00	0.03	0.05	17.77	0.02	41.00	0.00	0.01
F-02	ED	4	33.53	0.37	34.00	0.06	0.13	18.13	0.08	34.00	0.01	0.03
F-02	ED	5	32.78	0.25	16.00	0.06	0.13	18.25	0.05	16.00	0.01	0.03
F-02	ED	6	32.05	1.55	23.00	0.32	0.67	18.31	0.11	23.00	0.02	0.05
F-02	EN	1	35.18	0.36	17.00	0.09	0.18	18.02	0.09	17.00	0.02	0.04
F-02	EN	2	35.41	0.20	21.00	0.04	0.09	18.05	0.04	21.00	0.01	0.02
F-02	EN	3	34.87	0.25	28.00	0.05	0.10	17.98	0.03	28.00	0.01	0.01
F-02	EN	4	33.40	0.72	38.00	0.12	0.24	18.17	0.03	38.00	0.00	0.01
F-02	EN	5	32.02	0.26	14.00	0.07	0.15	18.30	0.02	14.00	0.01	0.01
F-02	EN	6	31.81	0.47	17.00	0.11	0.24	18.43	0.03	17.00	0.01	0.02

A.11 *Continued*

Month	Tide	Site	Mean	SD	n	SE	CI	Mean	SD	n	SE	CL
Salinity								**Temperature**				
F-02	FD	1	35.31	0.20	20.00	0.04	0.09	17.94	0.05	20.00	0.01	0.02
F-02	FD	2	35.14	0.33	18.00	0.08	0.16	17.91	0.10	18.00	0.02	0.05
F-02	FD	3	33.39	0.23	44.00	0.03	0.07	18.13	0.02	44.00	0.00	0.01
F-02	FD	4	-	-	-	-	-	-	-	-	-	-
F-02	FD	5	32.44	0.38	17.00	0.09	0.19	18.26	0.02	17.00	0.00	0.01
F-02	FD	6	31.19	0.37	17.00	0.09	0.19	18.44	0.02	17.00	0.01	0.01
F-02	FN	1	35.23	0.28	17.00	0.07	0.15	17.93	0.03	17.00	0.01	0.02
F-02	FN	2	34.91	0.44	28.00	0.08	0.17	18.02	0.05	28.00	0.01	0.02
F-02	FN	3	32.83	0.10	35.00	0.02	0.04	18.34	0.01	35.00	0.00	0.00
F-02	FN	4	32.23	0.09	21.00	0.02	0.04	18.39	0.01	21.00	0.00	0.01
F-02	FN	5	32.01	0.31	14.00	0.08	0.18	18.42	0.04	14.00	0.01	0.02
F-02	FN	6	31.15	0.56	21.00	0.12	0.25	18.56	0.12	21.00	0.03	0.06

A.12 Descriptive statistics of means for larval fish concentrations (numbers/100 m^3) collected during the 24-hour sampling regime carried out at the lower Tamar Estuary between December 2001 and February 2002. Abbreviations: D-01, December 2001; J-02, January 2002; F-02, February 2002; SD, standard deviation; SE, standard error, CI, confidence intervals.

Month	Tide	Mean	SD	n	SE	CI
Overall larval fish concentration						
D-01	ED	74.29	50.63	6	20.67	53.13
D-01	EN	172.19	123.09	6	50.25	129.17
D-01	FD	238.68	241.28	6	98.50	253.20
D-01	FN	117.08	74.93	6	30.59	78.63
J-02	ED	18.42	15.69	6	6.40	16.46
J-02	EN	55.45	48.51	6	19.80	50.91
J-02	FD	7.06	6.00	6	2.45	6.30
J-02	FN	35.61	29.53	6	12.05	30.99
F-02	ED	6.06	5.75	6	2.35	6.03
F-02	EN	133.09	144.24	6	58.89	151.37
F-02	FD	10.98	10.49	6	4.28	11.00
F-02	FN	6.01	3.41	6	1.39	3.58